University of Alberta

INTERACTIVE EFFECTS OF LOGGING AND SOLAR ULTRAVIOLET RADIATION ON STREAM ECOSYSTEMS

by

John James Clare

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

Environmental Biology and Ecology
Department of Biological Sciences

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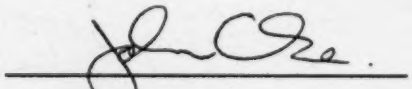

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The undersigned certify that they have read, and reccommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Interactive effects of logging and solar ultraviolet radiation on stream ecosystems** submitted by **John James Clare** in partial fullfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

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ABSTRACT

Since the discovery of the springtime Antarctic ozone hole in 1985, there has been increasing concern over the biological effects of stratospheric ozone depletion and increasing solar ultraviolet radiation (UV: 280-400 nm). Recent research has demonstrated that UV irradiance in freshwater ecosystems may also increase as a result of climate change and acid precipitation. Other anthropogenic stressors, such as nutrient enrichment and deforestation, may also increase the exposure of aquatic ecosystems to UV. In this study, we examine the interactive effects of UV radiation and nutrient enrichment on stream mesocosms in central British Columbia, Canada. We also examine the effects of UV and clear-cut logging on a stream ecosystem in the northern boreal region of British Columbia. Our results suggest that nutrient enrichment increases the algal biomass, thus providing a refuge for grazing invertebrates from UV exposure. We also found that the negative effects of logging and UV radiation varied within the same clear-cut, changing with distance downstream of the forest/clear-cut edge.

"One of the penalties of an ecological education is that one lives alone in a world of wounds... An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be a doctor who sees the marks of death in a community that believes itself well and refuses to be told otherwise."

– Aldo Leopold, 1953

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PREFACE TO THE THESIS

Most scientific endeavours require the collaboration of several individuals. This research is no exception. In recognition of the contribution others have made to this work, I have used the plural throughout my thesis. In addition, I have given credit by way of co-authorship to those individuals whom have made a significant contribution to chapters that have, or will be, submitted for publication.

Chapter 2:

Clare, J.J., D.J.Kelly, and M.L. Bothwell. Algal mats as a refuge from solar ultraviolet radiation for stream invertebrates. Submitted to:*The Journal of the North American Benthological Society.*

Chapter 3:

Clare, J.J., M.L. Bothwell, and D.W. Schindler. Interactive effects of clear-cut logging and solar ultraviolet radiation on a small stream.

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Chapter 1: GENERAL INTRODUCTION

The effect of solar ultraviolet radiation on aquatic ecosystems

Since the discovery of the springtime Antarctic ozone hole in 1985 (Farman *et al.* 1985), there has been concern over the biological effects of stratospheric ozone depletion and increasing ultraviolet radiation (UV: 280-400 nm). Losses of stratospheric ozone have been highest in the Antarctic, leading to increases in biologically active radiation at the earth's surface (McKinlay and Diffey 1987) of 5.5% decade^{-1} (Madronich *et al.* 1998). While much of the scientific focus on increasing UV has centered on Antarctica, biologically active radiation has also increased by 4.0 to 5.0% decade^{-1} at northern mid-latitudes (Kerr and McElroy 1993, Madronich *et al.* 1998). Recent research has demonstrated that freshwater ecosystems at these latitudes may be particularly vulnerable to increases in UV radiation due to interactions with other anthropogenic stressors. Climate change and acid precipitation increase exposure to UV by acting upon dissolved organic carbon (DOC), the primary attenuator of solar radiation in freshwaters (Schindler *et al.* 1996a, 1996b, Yan *et al.* 1996). Together, the "Three Prongs" of climate change, acidification, and ozone depletion (Gorham 1996) are significantly increasing the exposure of boreal freshwaters to UV (Schindler 1999), and consequently increasing its effect on sensitive freshwater systems. In addition to the "Three Prongs", other human caused disturbances, such as reservoir construction and clear-cut logging, may also increase the exposure of freshwater ecosystems to UV (Schindler 1998a).

The consequences of increased UV radiation on freshwater ecosystems include the inhibition of algal photosynthesis and reduced algal growth rates (Karentz *et al.* 1994, Herrmann *et al.* 1996, Häder *et al.* 1998). Ultraviolet radiation is sufficiently energetic to break apart DNA, and in algae, it disrupts the electron transport chain and photosystem II reaction centers (Häder *et al.* 1995, Karentz *et al.* 1994 Häder *et al.* 1998). In addition,

UV radiation may alter cell size, bleach cellular pigments, inhibit cellular orientation and mobility and reduce the uptake of inorganic nutrients (Bothwell *et al.* 1993, Karentz *et al.* 1994, Burma *et al.* 1995, Hessen *et al.* 1997, Häder *et al.* 1998). In cyanobacteria, nitrogen and CO_2 fixation are also affected by UV stress (Donkor and Häder 1996).

Ultraviolet radiation may also affect higher trophic levels and secondary production in three main ways. First, UV radiation may have direct negative effects on aquatic animals. For example, zooplankton (Williamson *et al.* 1994, Zagarese *et al.* 1998) benthic invertebrates (Bothwell *et al.* 1994, Kiffney *et al.* 1997, Donahue and Schindler 1998) fish (Williamson *et al.* 1997, 1999) and amphibian populations (Blaustein *et al.* 1997, Ovaska *et al.* 1997) have all demonstrated sensitivity to UV radiation. Secondly, UV radiation may indirectly influence secondary production through direct effects on primary production. For example, the growth and succession of periphytic and littoral algal communities has been shown to be depressed by exposure to UV (Bothwell *et al.* 1993, Vinebrooke and Leavitt 1996, 1999). This decrease in primary production may consequently lead to reduced food availability for higher trophic levels (Häder *et al.* 1995, 1998, Vinebrooke and Leavitt 1999). Third, grazers may also be affected by UV induced changes in the morphology and biochemistry of primary producers. UV exposure may reduce uptake of inorganic nutrients, changing the stoichiometry and nutrient quality of algal for grazers (VanDonk and Hessen 1995, Hessen *et al.* 1997). A number of experiments have found decreased fecundity and growth of zooplankton feeding on nutrient deficient algae (Sterner *et al.* 1993, Sterner and Hessen 1994). There is also evidence that exposure of algae to UV radiation may result in the intracellular accumulation of short-chained fatty acids (Hessen *et al.* 1997) which may also affect their quality for grazers. In addition, changes in algal cell motility and morphology may also affect consumption by grazers.

It is important to note that trophic level effects of UV exposure do not always follow a bottom-up pattern. In some circumstances, UV effects may "cascade" down

trophic levels (Bothwell *et al.* 1994, Williamson 1995). For example, Bothwell *et al.* (1994) found in small artificial streams, that the direct negative effect of UV on grazing larval chironomids was greater than the effect on algae. This resulted in lower grazing intensity and a net increase in algal biomass in streams exposed to UV radiation.

Ultraviolet radiation and nutrient enrichment

The concentration of inorganic nutrients may significantly interact with UV exposure at several ecological scales. As stated, UV radiation can inhibit the uptake of nitrogen and phosphorus by individual algal cells (Hessen *et al.* 1997), thus affecting their quality for grazers. In addition, the direct negative effects of UV exposure on algal physiology have been observed to vary with nutrient concentrations (Hessen *et al.* 1997, Vinebrooke and Leavitt 1998). In addition, nutrient concentration may also affect the UV sensitivity of whole ecosystems. For example, the absence of significant UV effects in more productive aquatic ecosystems has been reported previously (DeNicola and Hoagland 1996, Williamson *et al.* 1994, Zagarese *et al.* 1994). It is possible that high algal growth, successional rates, and species turnover rates typical of nutrient rich systems may offset the deleterious effects of UV exposure. It is also possible that changes in algal taxonomy, algal biomass, or algal mat thickness in benthic systems, associated with increased nutrients, may provide a physical refuge from UV exposure for other benthic organisms.

Ultraviolet radiation and clear-cut logging

The importance of watershed characteristics in the structure and function of stream ecosystems has long been recognized (Hynes 1975, Vannote *et al.* 1980). As interfaces between terrestrial and aquatic ecosystems, riparian zones are particularly important in regulating the effect of land use practices on streams. The riparian corridor encompasses the stream channel and the portion of the upland landscape that may be

affected by elevated water tables and flooding, and in turn affect the physical, chemical, and biological properties of the stream (Gregory *et al.* 1991, Naiman *et al.* 1993).

Clear-cut logging of stream watersheds, and in particular the destruction of riparian corridors, has dramatic consequences for stream ecosystems. Clear-cut logging can increase solar exposure (Naiman *et al.* 1992, Hetrick *et al.* 1998, Chen *et al.* 1999), increase water temperature (Brown and Krygier 1970, Lynch *et al.* 1984, Garman and Moring 1991), alter channel morphology (Heede 1991, Ryan and Grant 1991) increase sediment transport (Lisle 1982, Heede 1991) and increase concentrations of dissolved matter (Borman *et al.* 1974, Meyer and Tate 1983, Garman and Moring 1991). These logging induced changes may also significantly interact with UV exposure to produce other effects on stream biota. Obviously, the removal of riparian vegetation increases incident UV exposure. In addition, clear-cutting decreases long term export of DOC from the watershed (Meyer and Tate 1983), which may potentially increase UV penetration through the water column. However, logging induced nutrient enrichment (e.g., Hartman and Scrivener 1990) and potential increases in algal mat thickness (Borchardt 1996, Stevenson 1997) may offset the effect of increased UV exposure by providing physical refugia for other organisms.

Organization of the study

In this study, we conducted two separate experiments to examine the effects of UV radiation under different environmental conditions. We examined the interactive effects of UV radiation and nutrient enrichment, and the effects of UV radiation and clear-cut logging, on small boreal streams of north-central British Columbia, Canada. Headwater streams may be particularly vulnerable to UV exposure due to their shallow depths, relatively low DOC, and because they are highly influenced by the riparian corridor (Naiman *et al.* 1992, Chen *et al.* 1999). In addition, small streams are afforded less protection and narrower riparian buffer widths by provincial forest practices

guidelines (BC Ministry of Forests 1992), thus making them more vulnerable to the deleterious effects of clear-cut logging.

Previous work on the effects of UV radiation on boreal streams revealed that when benthic algal biomass was high, invertebrate grazers did not respond to the presence or absence of UV (W.F. Donahue, University of Alberta, personal communication). Based on these observations, we hypothesized that nutrient enrichment, and the resulting increase in algal biomass, may provide a physical refuge for some invertebrates from UV exposure. Chapter 2 addresses this hypothesis by examining the response of benthic invertebrates to UV in nutrient enriched or control stream mesocosms with high or low algal biomass.

While the results of mesocosm experiments are useful in examining the effect of one or two manipulations in a controlled environment, they often lack the complexity and realism of whole ecosystems (Schindler 1998b). As a result, we conducted a large scale experiment in a natural stream to examine the interactive effects of clear-cut logging and UV on a benthic stream ecosystem. In cooperation with the Department of Fisheries and Oceans, Stuart-Takla Fish/Forestry Interaction Study, we manipulated UV exposure in logged and unlogged reaches of Baptiste Creek the summer immediately following clear-cutting. This allowed us to test the following set of hypotheses: (1) that clear-cut logging would increase the exposure of the stream to UV; (2) that exposure to increased UV would significantly affect benthic communities in logged reaches; and (3) that the effect of increased UV exposure would be in addition to other effects of logging. These hypotheses are addressed in Chapter 3.

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Chapter 2: Algal mats as a refuge from solar ultraviolet radiation for stream invertebrates

INTRODUCTION

Relatively small increases in nutrient concentrations can lead to dramatic increases in the biomass and alter the structure of benthic algal mats (Bothwell 1989, Borchardt 1996, Stevenson 1997). Such algal mats can have a complex, three dimensional structure analogous to terrestrial forests, where prostrate diatoms cover the substrate like a turf, stalked diatoms comprise the understory, and long filamentous algae form an effective canopy (Hoagland 1982, Steinman 1996, Tuchman 1996, Stevenson 1997). The physical structure of benthic algal mats often has profound consequences for the algal cells in the understory and for benthic invertebrates inhabiting the mat. The filamentous canopy may intercept light (Kühl and Jørgensen 1992, Dodds 1992, Tuchman 1996) and restrict nutrient uptake within the mat by creating an unmixed boundary layer, separating the understory from the bulkwater nutrient source (Jørgensen and Revsbech 1985, Stevenson and Glover 1993, Borchardt 1996). The shift in physiognomy from films to filamentous mats also has direct effects on the herbivore community, favoring gatherers and shredders (Steinman 1996, Stevenson 1997) and more mobile caddisflies (Dudley *et al.* 1986) while having a negative effect on scrapers and smaller sessile grazers (Creed 1994, Steinman 1996). In addition, thick mats of filamentous algae may indirectly benefit smaller grazing invertebrates by providing refugia from predation. For example, the filamentous green algae *Cladophora* has been shown to provide protection from predation for isopods and chironomids (Holomuzki and Short 1988, Power 1990).

The dense canopy provided by filamentous algae may also provide a refuge from exposure to solar ultraviolet radiation (UV: 280-400 nm). Recent evidence shows that aquatic ecosystems may be exposed to increasing levels of UV radiation. Between 1989

and 1993, the loss of stratospheric ozone at northern mid latitudes resulted in increases of UVB radiation (280-320 nm) of 35 percent (%) per year in winter and 7% per year in summer (Kerr and McElroy 1993). Potentially more significant, the depletion of dissolved organic carbon (DOC), the primary attenuator of UV in freshwater ecosystems (Scully and Lean 1994, Kirk 1994), may increase UV exposure in boreal freshwaters several-fold (Schindler *et al.* 1996). Another factor regulating exposure of aquatic communities to UV may be external shading by riparian forests (DeNicola and Hoagland 1992).

Current levels of UV radiation have significant consequences for both lake (Williamson *et al.* 1994, Vinebrooke and Leavitt 1996, 1998, 1999, Zagarese *et al.* 1998) and stream (Bothwell *et al.* 1993,1994, Kiffney *et al.* 1997a, 1997b, Donahue and Schindler 1998) ecosystems. While the direct effects of UV exposure on organisms have been extensively documented (e.g., Häder *et al.* 1995, 1999) complex ecosystem responses to UV radiation remain unclear (Bothwell *et al.* 1994, Williamson 1995). Indirect effects of UV exposure, as well as interactive effects with other environmental conditions, have the potential to produce far reaching ecosystem scale changes.

The objective of this study was to test for the interaction between UV radiation and nutrient enrichment in small stream mesocosms. We tested the hypothesis that changes in algal biomass and assemblage structure associated with nutrient enrichment would produce an algal canopy sufficient to shade invertebrate grazers from UV exposure.

MATERIALS AND METHODS

The extent to which standing algal biomass provides a refuge for larval chironomids from UVR was examined between 1 June and 25 July 1996 at the Experimental Troughs Research Apparatus (EXTRA) in Chase, British Columbia, Canada. EXTRA is located along the South Thompson River near the outlet of Little

Shuswap Lake (50°49'35"N, 119°41'5"W). Twelve parallel Plexiglas troughs, each 2 m long by 19 cm wide, were continuously fed unfiltered river water from a constant pressure headtank. Flow was adjusted in each trough to 50 L min^{-1}, resulting in a water depth and velocity of approximately 1 cm and 50 cm s^{-1} respectively. Sheets of open-cell Styrofoam-DB lined the bottom of each trough and served as a substratum for algal and invertebrate colonization. Details of the construction and operation of this research facility are given elsewhere (Bothwell 1988).

Previous experiments at the EXTRA facility have demonstrated that periphyton growth rates and biomass are phosphorus limited (Bothwell 1988, 1989). Algal biomass was therefore augmented in six troughs by continuous additions of 5.0 µg P L^{-1} (K_2HPO_4), while the remaining six troughs received no nutrient additions. Troughs receiving P additions were precolonized with algae for 21 days prior to UV manipulation, beginning June 17. Troughs with ambient P concentrations began precolonization 7 days later on June 24, 14 days prior to the start of the experiment. During the entire algal colonization phase, periodic additions of the insecticide Malathion (Dimethoxyphosphinothioyl thiobutanedioic acid diethyl ester) where made to the troughs. This effectively prevented colonization by larval chironomids (Bothwell *et al.* 1994). Previous research has shown that Malathion in insecticide-diffusing substrata may also significantly decrease algal biomass accrual, especially under conditions of enhanced nutrient supply (Francoer *et al.* 1999). However, we used short term, periodic additions of the insecticide to remove invertebrates. This was done specifically to avoid the effects of long-term, chronic exposure of Malathion on algae. All flumes were precolonized in the presence of ambient levels of solar UV radiation.

Malathion additions ceased on July 9, allowing chironomid larvae to begin colonizing the flumes naturally from populations suspended in the river water. On the same day, exposure of the flumes to UVR was manipulated by covering the flumes with either UV transparent (acrylic type OP4 Plexiglas; CYRO; 70 to 90% transmittance

throughout the UVB and UVA) or UV opaque (acrylic type UF4 Plexiglas; Rohm and Hass; 50% transmission at 318 nm) shields. All flume covers transmitted ~90% of photosynthetically active radiation (PAR: 400-700 nm) (Fig. 2.1). The combination of nutrient and light manipulations resulted in three replicates of four different treatments: (+Nutrient +UV); (+Nutrient –UV); (–Nutrient +UV); and (–Nutrient –UV).

The time course accrual of algal biomass was measured by Chl *a* concentration. Samples were taken every 7 days by removing triplicate 5 cm^2 cores from the Styrofoam substrate in each flume. Chlorophyll was extracted using 90% ethanol (Webb *et al.* 1992) and measured fluorometrically on a Turner Designs 10au fluorometer (Holm-Hansen *et al.* 1978). On day seven of the experiment, an additional core was taken to microscopically examine the taxonomic structure of the algal community.

Chironomid larvae were also sampled every 7 days by removing a 190 cm^2 section of substratum from each flume. Organisms were removed by placing the Styrofoam in filtered river water and shaking it vigorously for five minutes. The slurry was filtered through a 80 µm sieve and the contents preserved in 70% ethanol for later enumeration in the laboratory. Chironomid fauna dominant at the EXTRA are from the subfamily Orthocladiinae: *Cricotopus* and *Orthocladius* (Bothwell *et al.* 1994).

Photosynthetically active radiation was continuously logged at hourly intervals throughout the entire experiment with a Li-Cor LI-1000 data logger equipped with a quantum cosine sensor (LI 190SA). Estimates of UVB radiation were obtained from a linear regression of simultaneous PAR and UVB measurements made at the EXTRA facility during 1991, 1993, and 1994 (r^2=0.838; Fig. 2.2). During this period PAR was measured with the same instrument and UVB measured with a Brewer Ozone Spectrophotometer (SCI-TEC Instruments, Saskatoon, Saskatchewan, Canada).

During the experiment, total daily fluxes of PAR ranged from 12.4 to 58.2 E m^{-2} d^{-1} and averaged 40 E m^{-2} d^{-1} (Fig. 2.3). Solar UVB fluxes varied considerably from day to day with a mean of 53.9 kJ m^{-2} d^{-1} and a range of 33.2 to 64.2 kJ m^{-2} d^{-1} (Fig.

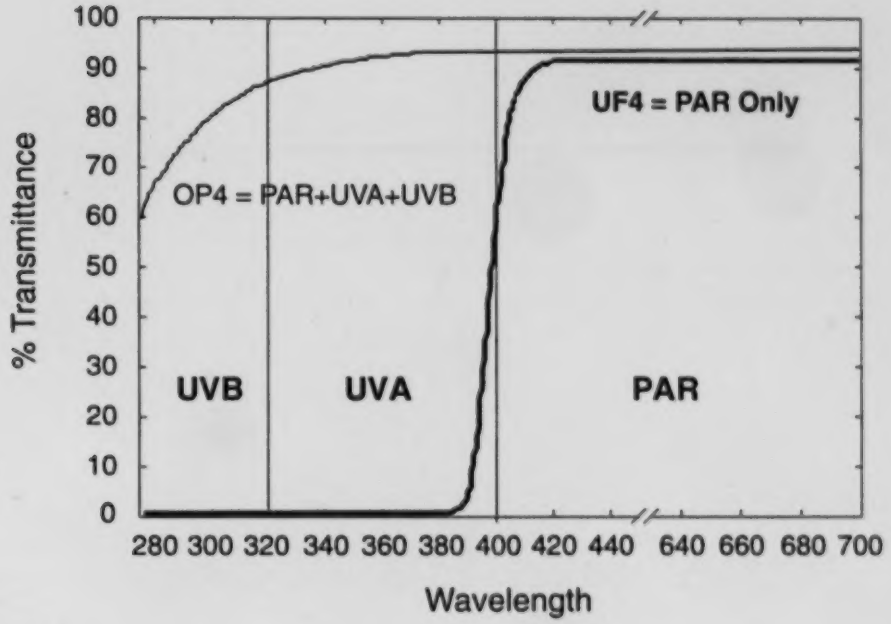

Figure 2.1: Spectral transmittance profile (280 to 700 nm) through UV-transmitting (OP4; PAR+UV) and UV-opaque (UF4; PAR Only) Plexiglas sheets.

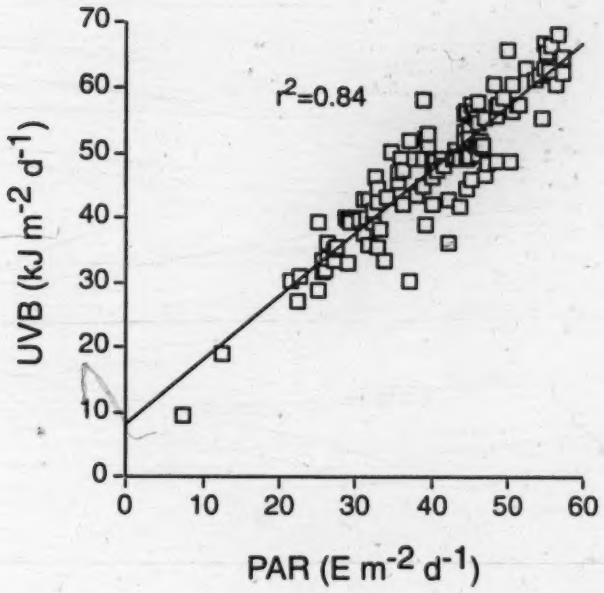

Figure 2.2: Relationship between photosynthetically active radiation (PAR) and ultraviolet-B radiation (UVB) at the EXTRA facility during the summers of 1991, 1993, and 1994. A linear model with r^2=0.84, was used to predict UVB levels in Figure 2.3.

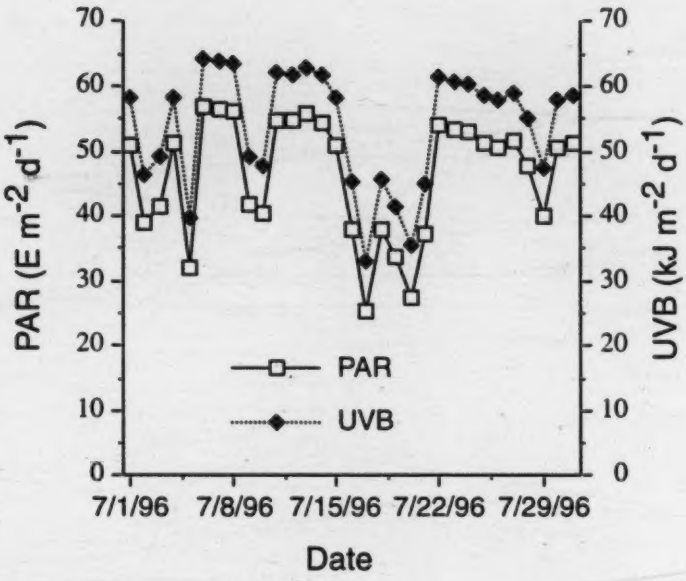

Figure 2.3: Mean daily PAR (E m^{-2} d^{-1}) and UVB (kJ m^{-2} d^{-1}) fluxes during the experimental period. PAR levels were continuously measured during the experiment, while UVB fluxes where estimated from PAR measurements using the linear model in Figure 2.2.

2.3). These levels of solar radiation were similar to those previously observed to cause deleterious effects on stream communities at the EXTRA facility (Bothwell *et al.* 1993, 1994).

Statistical analysis was conducted using SPSS (ver. 6.1, 1995, SPSS Inc.). To determine differences in chironomid abundance between the four treatments, a two-way repeated measures analysis of variance (RM-ANOVA) was used (Krebs 1989, Norris and Georges 1993). Parametric assumptions where met using a ln (n+1) transformation (Zar 1996).

RESULTS

The addition of phosphorus to the experimental flumes significantly increased algal biomass (Nutrient $P<0.0001$; Table 2.1). Over the course of the experiment, Chl *a* was approximately 600% greater in the +Nutrient than the –Nutrient treatment (Fig 2.4). The increase in periphyton biomass in P enriched flumes resulted from a large change in the algal assemblage. On day seven of the experiment, non-enriched flumes were dominated by diatoms (Fig. 2.5) with *Achnanthes minutissima*, *Fragilaria crotonensis*, *F. vaucheriae*, and *Tabellaria fenestrata* and *Hannea arctus* most common (Table 2.2). Phosphorus-enriched flumes were instead dominated by filamentous green algae (Fig. 2.5) with *Odegonium spp.* and *Stigeoclonium spp.* dominating (Table 2.2). Total cell

Table 2.1: Repeated-measures ANOVA for the effects of ultraviolet radiation (UV) and nutrient additions (Nutrient) on log-transformer Chl *a* values.

Source	df	*F*–statistic	*P*–value
UV	1	0.25	0.63
Nutrient	1	347.41	< 0.0001
UV x Nutrient	1	0.13	0.73
Time	2	16.39	< 0.0001
Time x UV	2	0.23	0.80
Time x Nutrient	2	2.70	0.10
Time x UV x Nutrient	2	0.32	0.73

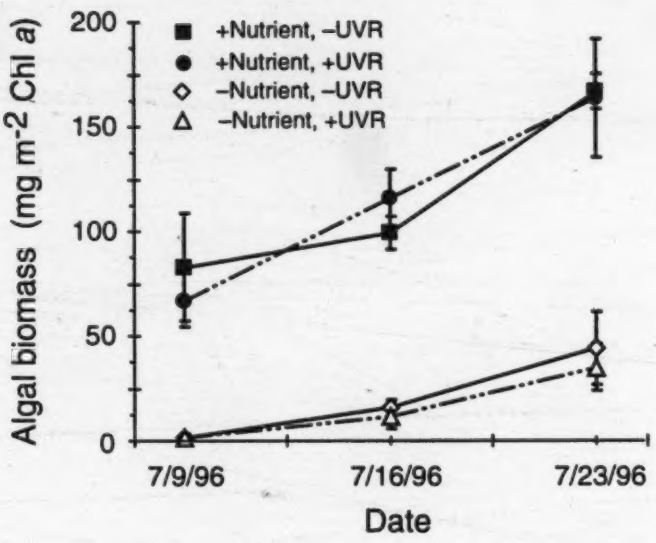

Figure 2.4: Algal biomass (Chl *a*) in the +Nutrient (solid symbols) and –Nutrient treatments (open symbols). Error bars are ± S.D. (n=3).

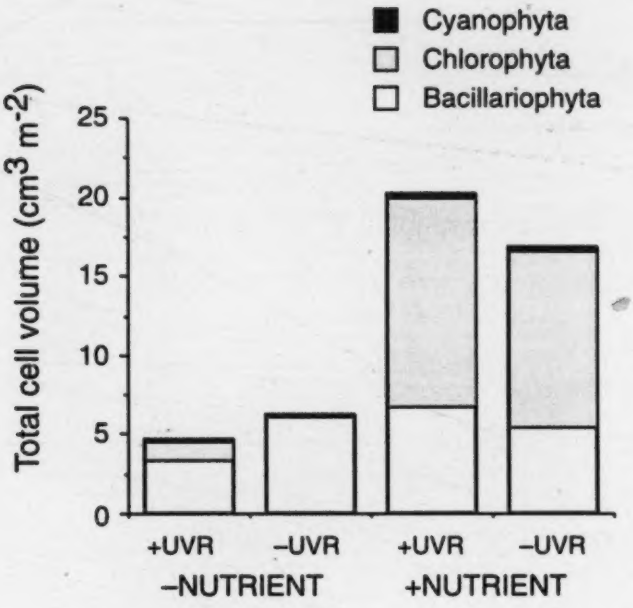

Figure 2.5: Taxonomic character of the algal community in the four treatments on day seven (July 16) of the experiment by total cell volume (n=1). See text for detailed descriptions of major taxa in each family.

Table 2.2: Percent total biomass of dominant algal taxa in each of the treatments on day 7 of the experiment (n=1).

	Nutrient Control		Nutrient Enriched	
	+UV	–UV	+UV	–UV
Achnanthes minutissima	2.5	0.8	0.3	0.4
Fragilaria crotonensis	16.6	12.0	1.2	1.2
Fragilaria vaucheriae	14.8	9.2	1.4	1.3
Tabellaria fenestrata	12.8	34.4	0.9	1.2
Hannaea arcus	17.2	23.0	16.0	13.2
Total Bacillariophyta	**72.3**	**99.3**	**33.4**	**32.3**
Total Cyanobacteria	**1.8**	**0.7**	**1.1**	**1.7**
Odegonium spp.	0.0	0.0	28.8	0.0
Stigeoclonium spp.	0.0	0.0	21.6	66.0
Total Chlorophyta	**25.8**	**0.0**	**65.4**	**66.0**

volumes of diatoms were similar between the two nutrient treatments (Fig. 2.5).

Removal of UVR had no effect on periphyton biomass during the experimental period (Fig 2.4). There was no significant difference in Chl *a* between the +UVR and –UVR treatments (UV P=0.63; Table 2.1). In addition, the lack of a UV effect on Chl *a* was consistent in both the enriched and unenriched flumes (UV x Nutrient P=0.73; Table 2.1).

Larval chironomids responded differently to UV radiation in the two nutrient treatments (UV x Nutrient P=0.011; Table 2.3). In the unfertilized flumes, chironomid density was significantly lower when exposed to UV radiation (Fig. 2.6a). However, in

Table 2.3: Repeated-measures ANOVA results for the effects of ultraviolet radiation (UV) and high algal biomass (Nutrient) on log-transformed chironomid abundance.

Source	df	F–statistic	P–value
UV	1	11.00	0.011
Nutrient	1	31.83	< 0.001
UV x Nutrient	1	11.05	0.011
Time	2	281.58	< 0.0001
Time x UV	2	9.29	0.0021
Time x Nutrient	2	12.59	< 0.001
Time x UV x Nutrient	2	7.20	0.0059

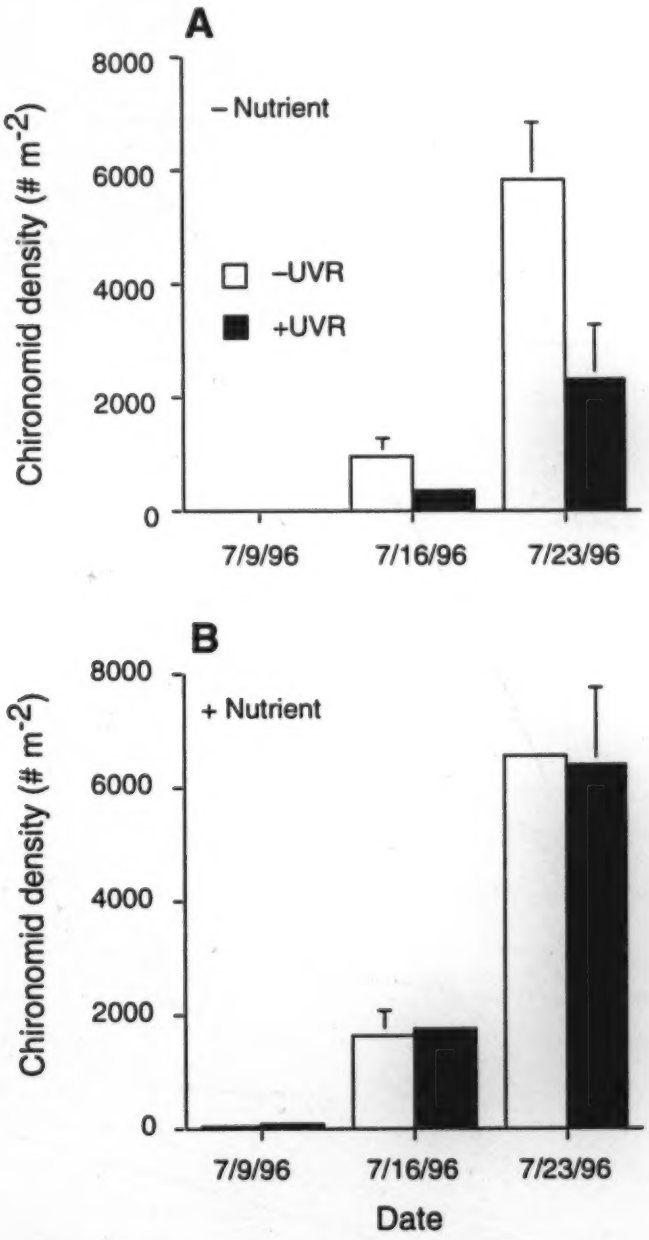

Figure 2.6: Total chironomid density in the (A) –Nutrient and (B) +Nutrient treatments under UV shielded (white) and UV exposed (black) conditions. Error bars are ± S.D. (n=3).

the nutrient enriched flumes, where algal biomass was higher and filamentous algae dominated, chironomid larvae did not respond to the presence or absence of UV light (Fig. 2.6b). Chironomids did not respond to nutrient enrichment and increased algal biomass in the absence of UV light. There was no difference in chironomid abundance between the +Nutrient and –Nutrient treatments shielded from UV (Fig. 2.6).

DISCUSSION

The increase in algal biomass caused by phosphorus enrichment resulted in UV radiation having little effect on chironomid density. In contrast, the suppression of chironomid colonization by UV radiation in the unenriched flumes was consistent with earlier work, where both UVA and UVB radiation significantly inhibited invertebrate colonization in streams with lower algal biomass (Chl *a* <100 mg m^{-2}; Bothwell *et al.* 1994).

This study demonstrates that habitat structure may shield organisms from UV exposure. Other physical and chemical components of aquatic habitats have been observed to significantly affect biotic responses to UV. For example, water depth (Williamson *et al.* 1994, Millot-Roy and Vincent 1994), vertical migration of zooplankton (Williamson 1995, Zagarese *et al.* 1998) and dissolved organic carbon (Williamson *et al.* 1996, Schindler *et al.* 1996, Vinebrooke and Leavitt 1998) have been observed to affect community response to UV radiation. Other habitat characteristics which may affect benthic community response to UV include the size and shape of substrata, flow conditions in lotic habitats, and other aspects of water chemistry, such as photolytic production of hydrogen peroxide (Scully *et al.* 1996) or heavy metal concentrations (Häder *et al.* 1999).

Differences in habitat structure may help explain why UV effects have varied between studies. The effects of UV radiation have been greater in studies where habitat structure is relatively simple, as in laboratory experiments under strict controlled

conditions (e.g., Kiffney *et al.* 1997b, Hurtubise *et al.* 1998), than in studies of natural, structurally complex systems (e.g., Kiffney *et al.* 1997a, Vinebrooke and Leavitt 1996, 1998). For example, Hurtubise *et al.* (1998) found *Daphnia* to be highly sensitive to UV light in laboratory experiments using a solar simulator, while Zagarese *et al.* (1994) reported varying sensitivity in natural lakes.

Primary productivity, food web structure and trophic relationships may also influence how components of a community respond to UV exposure (Williamson *et al.* 1995). The absence of significant UV effects on more productive aquatic communities has been reported previously (DeNicola and Hoagland 1996, Williamson *et al.* 1994, Zagarese *et al.* 1994). Williamson *et al.* (1994) found zooplankton held in the surface waters of clear oligotrophic lakes were significantly inhibited by ambient levels of UVB radiation, while zooplankton simultaneously incubated in a eutrophic lake were not. Similarly, DeNicola and Hoagland (1996) found no significant effect of UV radiation on benthic macroinvertebrate or periphyton communities in a nutrient rich prairie stream. It is possible that the high algal growth, successional rates, and species turnovers typical of nutrient rich systems may offset the deleterious effects of UV exposure.

In many aquatic ecosystems, herbivores regulate algal biomass and marginal increases in nutrient availability may have little impact on algal biomass accumulation or assemblage physiognomy (Steinman 1996). When nutrient availability causes algal production rates to exceed herbivory rates, shifts in algal biomass and assemblage structure occur (Stevenson 1997). Our results and previous examinations of nutrient dynamics in streams (Bothwell 1989, Borchardt 1996) demonstrate that relatively small increases in nutrient concentrations can lead to large changes in algal biomass accumulation and species composition. As a result, eutrophication may decrease the sensitivity of many freshwater communities to UV exposure.

Benthic communities may also become less sensitive to UV radiation as they reach later successional stages. Succession in algal mats may lead to a directional change

in structure from low to high physical stature, and from small sessile, to larger, motile species (Hoagland *et al.* 1982, Steinman 1996). Shifts in algal assemblages from prostrate to more filamentous species may increase shading effects. Smaller, earlier successional species exhibit greater UV sensitivity (Bothwell *et al.* 1993, Vinebrooke and Leavitt 1996) than do later, larger celled species. Thus, later successional stages may provide better shading from UV for other members of the benthic community.

Differences in community succession may therefore explain why studies employing precolonized artificial substrata did not show clear effects of UV light (Vinebrook and Leavitt 1998, Hill *et al.*1997) as experiments which employed clean, uncolonized substrata (Bothwell *et al.* 1993, 1994, Vinebrooke and Leavitt 1996, Kiffney *et al.* 1997a). In natural systems, successional stage is dynamic, depending on productivity, the rate of succession, herbivore interactions and on the frequency of disturbance which resets the community. As a result, the role that community succession plays in mitigating UV damage will also be dynamic.

Trophic interactions may also influence community responses to UV. Bothwell *et al.* (1994) found that high sensitivity of grazing chironomids to UVB resulted in increased algal biomass in habitats exposed to UVB radiation, even though UVB is known to suppress algal photosynthesis, cell division, and growth rates (Behrenfeld *et al.* 1992, Bothwell *et al.* 1993, Cullen and Neale 1994). The strong effect of UVB on the chironomids led to a release in the intense grazing pressure, resulting in a counter-intuitive increase in algal biomass in the UV exposed habitat.

The character of the herbivore community and the resulting interaction with the algal mat may also determine whether or not nutrient enrichment or community maturity influence UV effects in benthic ecosystems. The presence of macroinvertebrate herbivores that selectively target canopy forming algal species may greatly reduce the interaction between UV, algal mats, and herbivores. For example, Hart (1985) found that *Leucotrichia* selectively removed filamentous algae from its territory, perhaps to maintain

higher densities of understory food sources. Selective removal of the algal canopy would result in a loss of shading, independent of nutrient levels, productivity, or successional stage. In addition, the presence of certain herbivores at early stages of community development may influence the outcome of nutrient enrichment, community succession and UV interactions. For example, Dudley and D'Antonio (1991) found that if grazers were present, colonization of the filamentous chlorophyte *Cladophora* could be prevented.

Clearly, the response of benthic communities to UV radiation will be influenced by nutrient status. As a result, short term measurements of UV induced inhibition at single trophic levels, or in simplified laboratory experiments, may not accurately predict the response of whole communities.

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Chapter 3: Interactive effects of clearcut logging and solar ultraviolet radiation on a small stream

INTRODUCTION

The ecological health and stability of streams and rivers are intimately linked to the surrounding terrestrial ecosystem by riparian zones. Destruction or alteration of riparian zones through forestry activity can affect many physical, chemical, and biological properties of the stream. Clear-cut logging may change solar exposure (Brosofske *et al.* 1997, Hetrick *et al.* 1998a, Chen *et al.* 1999), thermal regime (Brown and Krygier 1970, Lynch *et al.* 1984, Holtby 1988, Garman and Moring 1991, Hetrick *et al.* 1998a), flow levels (Lisle 1982), channel width and depth (Heede 1991, Ryan and Grant 1991), sediment transport (Lisle 1982, Heede 1991) and concentrations of suspended and dissolved matter in the stream (Hobbie and Likens 1973, Borman *et al.* 1974, Meyer and Tate 1983, Garman and Moring 1991). These changes in physical and chemical character may in turn lead to large changes in benthic algal (Stockner and Shortreed 1976, Lowe *et al.* 1986, Robinson and Rushforth 1987, Hetrick *et al* 1998a) and invertebrate (Newbold *et al.* 1980, Murphy and Hall 1981, Carlson *et al.* 1990, Brown *et al.* 1997, Hetrick *et al.* 1998b) productivity and assemblage composition.

Several studies have examined the effect of riparian logging and forest canopy removal on increasing the exposure of streams to solar radiation (Robinson and Rushforth 1987, Hetrick *et al.* 1998a). However, none of these studies have specifically examined the effect of increased ultraviolet (UV) radiation. Current levels of UV may have significant consequences for aquatic ecosystems, either through direct sensitivity of organisms to exposure (eg: Bothwell *et al.* 1993,1994, Karentz *et al.* 1994, Häder *et al.* 1995, 1998) or indirectly through altered trophic (Bothwell *et al.* 1994, Hessen *et al.* 1997, Williamson *et al.* 1999) or chemical (Scully *et al.* 1996, Häder *et al* 1998, Zepp *et*

al. 1998) interactions. The loss of stratospheric ozone in the northern hemisphere has resulted in an estimated 4-7% decade^{-1} increase in biologically active radiation reaching the earth's surface since the 1970's (Kerr and McElroy 1993, Madronich *et al.* 1998). In aquatic ecosystems, degradation or loss of dissolved organic carbon (DOC) results in increased penetration of UV through the water column (Schindler *et al.* 1996, Williamson *et al.* 1996, Yan *et al.* 1996). For example, decreases in DOC caused by localized climate warming and acidification resulted in several times more UV reaching boreal lake communities than did increases in UVB from ozone depletion (Schindler *et al.* 1996, Donahue *et al.* 1998). Clear-cut logging of riparian forests along streams, and other alterations of the local environment, may also increase the exposure of certain aquatic ecosystems to UV radiation (Schindler 1998).

The objective of this study was to examine the effect of clear-cut logging on a headwater boreal stream ecosystem. Specifically, we examined the effect of logging on solar exposure (including UV radiation), water temperature, and dissolved nutrients in logged and unlogged reaches of the same stream. We then examined the influence of these changes on the productivity and composition of benthic algal and invertebrate communities. We tested the following hypotheses: (1) that clear-cut logging and removal of the forest canopy would increase solar exposure, stream temperature, and nutrient loads, (2) that these changes would lead to large changes in the production and composition of benthic periphyton and invertebrate communities, and (3) that exposure to UV would significantly affect benthic communities in logged reaches of the stream.

MATERIALS AND METHODS

Study Site

Baptiste Creek (54°59'N, 125°32'W, 1300 m asl) is a first order tributary to the Stuart-Takla River System, situated in North-Central British Columbia, Canada (Fig. 3.1). The watershed is part of the northern limit of the Sub-boreal Spruce biogeoclimatic zone (B.C. Ministry of Forests and Lands 1988). Riparian forests are dominated by Subalpine Fir (*Abies lasiocarpa*), White Spruce (*Picea glauca*) and Lodgepole Pine (*Pinus contorta*). Terrain throughout most of the watershed is bedrock controlled, including hummocks and glacial lineations (Collett and Ryder 1997). This small creek (Table 3.1) is groundwater fed and experiences high flows during spring snow melt and summer rain events (Beaudry 1998). During the remainder of the summer the stream remains near baseflow, except during prolonged periods of drought when it may become intermittent. Baptiste Creek is naturally fishless.

Experimental Design

During the winter of 1996/1997 the Baptiste Creek watershed was commercially logged (Table 3.1). Sixty hectares of the 150-hectare watershed were clear-cut, resulting in over half of the total channel length running through the cut-block. A Riparian Management Zone (RMZ) was left along side the stream channel as prescribed by the British Columbia Forest Practices Code (B.C. Ministry of Forests 1995) which legislates the width and character of riparian buffers left along streams on public land. A 20 m RMZ of non-merchantable timber (diameter at breast height <15 cm for *P. contorta* and <20cm for *P. glauca* and *A. lasiocarpa*) was left along each side of Baptiste Creek. Heavy machinery was permitted to work within 5 m of the stream channel to remove merchantable timber, resulting in significant alteration of understory vegetation. Despite the application of these management practices, the retention of only non-merchantable

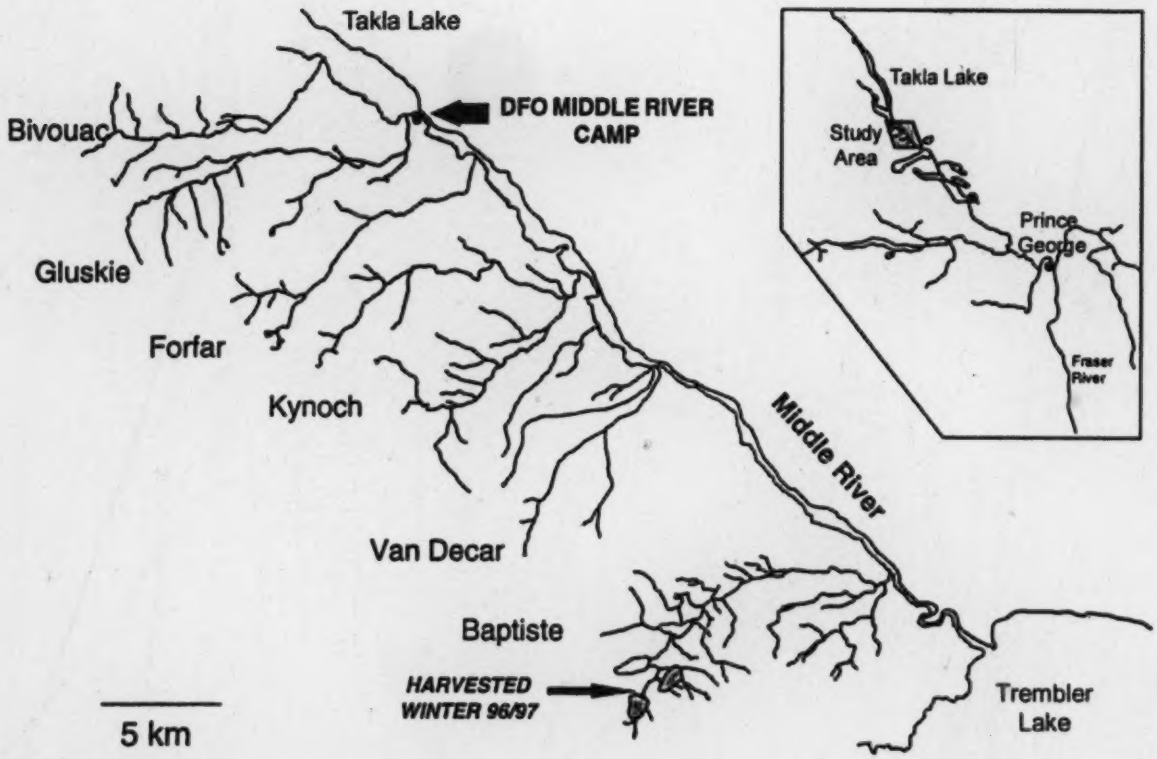

Figure 3.1: Map of the Stuart-Takla study area in North-Central British Columbia, Canada.

Table 3.1: Physical characteristics of the Baptiste watershed and details of logging treatment.

Feature	Value
Aspect	North
Elevation range (m asl)	980-1300
Watershed size (ha)	150
Area of watershed harvested (ha)	60
Total channel length (m)	2093
Length of channel harvested (m)	1060
Average channel gradient (%)	6.7
Channel gradient within cutblock (%)	4.8
Average channel width (m)	1.4

trees within the RMZ resulted in significant disturbance along the entire stream channel (Plate 4.1).

The effect of the winter harvest on Baptiste Creek was examined during July and August of 1997. A 3x2 factorial experiment considered three logging treatments (unlogged reference, top of clear-cut, and bottom of clear-cut) and two light treatments (photosynthetically active radiation (PAR) +UV or PAR –UV). Paired light treatments were replicated four times in the unlogged reference (500-250 m upstream of the forest/ clear-cut edge), and twice at each of the clear-cut sites (top of the clear-cut = 150-200 m downstream of the forest edge; bottom of the clear-cut = 500-600 m downstream of the forest edge) for a total of 16 replicates and 6 treatments. The unbalanced design resulted unintentionally when it became apparent that the effect of logging on the stream was different at the top and bottom of the clear-cut.

The two light treatments were established by placing large UV filters across the entire stream channel, 10 to 20 cm above the water surface. Acrylic sheets that either transmitted full spectrum solar radiation (Acrylite OP4; CRYO Industries) or excluded solar UV (Plexiglas UF4; Rohm and Hass) were fastened to 1.22 x 1.22 m wooden frames which were suspended with rebar from the stream bank. Acrylite OP4 transmitted 70 to 90% of total solar radiation below 400 nm (Bothwell *et al.* 1994) (Fig. 3.2). Plexiglas UF4 blocked out both UVA and UVB radiation (50% cutoff = 398 nm)

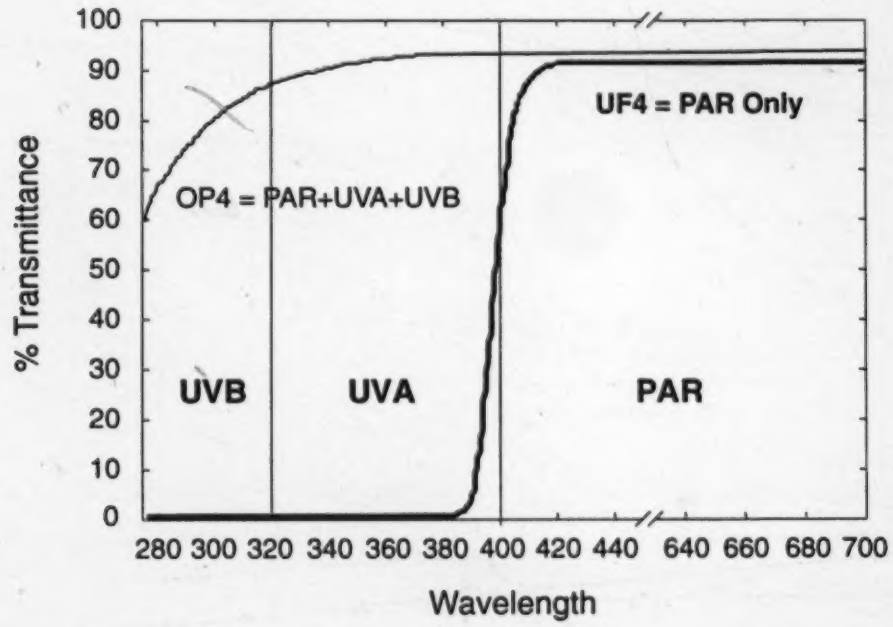

Figure 3.2: Spectral transmittance profile (280 to 700 nm) through UVR-transmitting (OP4; PAR+UVR) and UV-opaque (UF4; PAR Only) Plexiglas sheets.

(Bothwell *et al.* 1994). UVR filters were placed in random order over the stream channel at each site.

Under each screen 6 plastic trays (25 x 15.5 x 6 cm) filled with uncolonized, clean gravel substrate were placed to lie flush with the streambed. Benthic communities were permitted to naturally colonize the trays undisturbed until sampling.

Sampling Protocol and Analysis

Solar radiation was continuously recorded in the unlogged reference and bottom clear-cut sites. Photosynthetically active radiation (PAR) was measured at hourly intervals with a Li-Cor quantum cosine sensor (LI 190SA), and UVA and UVB radiation were measured with Vital Technology BW20 sensors. Data were logged with a Li-Cor LI-1000 data logger. A substantial period of data was lost during the 1997 experiment due to a recording error. As a result, PAR, UVA, and UVB were again recorded at the same locations during June and July 1998.

Stream temperature was also continuously recorded in the unlogged reference, top clear-cut and bottom clear-cut sites. Temperature was recorded with a Li-Cor sensor at the unlogged reference and bottom clear-cut sites, and with two Hobo Temp thermisters (Onset Computer Corporation) at the top clear-cut site. Due to the same recording error, temperature data at the upstream reference and bottom clear-cut sites were lost for part of the 1997 experiment. As a consequence, temperature was again measured during 1998 and these data used to construct a multiple regression model to estimate 1997 temperatures (upstream reference r^2=0.88; bottom clear-cut r^2=0.93).

Total dissolved phosphorus, total dissolved nitrogen, nitrate, DOC, alkalinity, and stream pH were all measured upstream of the clear-cut and within the clear-cut at 2 week intervals. Measurements of DOC concentration and fluorescence were used to estimate the attenuation of UVA and UVB radiation within the water column (Scully and Lean 1994).

The benthic community was sampled every two weeks by removing a substrate-filled tray from under each UV shield. Chlorophyll *a* was sampled by vigorously scrubbing, with a hard bristled toothbrush, triplicate, randomly selected 3.8 cm^2 areas on the upper surface of large cobbles. The resulting slurries were then filtered onto Whatman GF/C filters, transferred to dark petri-dishes and frozen. Chlorophyll *a* was extracted using 90% ethanol (Webb *et al.* 1992) and measured fluorometrically on an Turner Designs 10au fluorometer (Holm-Hansen *et al.* 1978). An additional 3.8 cm^2 area was sampled and preserved in Lugol's solution to microscopically examine the taxonomic structure of the algal community. The remaining substrate was washed in a plastic bucket and sieved through a 250 µm mesh. Organisms retained on the sieve were preserved in 70% ethanol.

Light microscopy was used to examine major algal groups during day 42 of the experiment. Aliquots of the preserved samples were allowed to settle overnight in sedimentation chambers (Lund *et al.* 1958). Counting units were individual cells, filaments or colonies depending on the organization of the algae. The algal units were counted from three or more transects on an inverted microscope. A minimum of 400 units were counted for each sample. Fresh weight biomass was calculated from recorded abundance and specific biovolume estimates, based on geometric solids (Rott 1981), assuming unit specific gravity. Biovolume of each species was estimated from the average dimensions of 15 to 20 individuals. The biovolumes of colonial taxa were based on the number of individuals in a colony. All calculations for cell concentration and biomass were performed with Hamilton's (1990) computer program.

Further processing was required to identify the majority of diatoms to the species level. A subsample was first boiled in 30% hydrogen peroxide for 45 minutes and washed several times with distilled water. A few drops of the diatom slurry were placed on a cover slip and allowed to evaporate overnight. Once dry, it was mounted in Naphrax and the diatoms were identified at 1000X magnification. The diatom taxa counted in the

fresh samples were then matched with those identified in the mounted sample.

Taxonomic identifications were based primarily on Anton and Duthie (1981), Findlay and Kling (1976), Prescott (1982), Whitford and Schumacher (1984), Krammer and Lange-Bertalot (1986, 1988, 1991a,b).

All invertebrates collected on a 1 mm sieve were identified and enumerated by light microscopy. Invertebrates were counted with a Wild M8 dissecting microscope. All insects were identified to the lowest taxonomic level (Resh and Jackson 1993) (usually family or genus level), except dipterans, which were only identified to family. Identifications were done using keys by Clifford (1991), and Merritt and Cummins (1996).

Statistical Analysis

Repeated-measures analysis of variance (RM-ANOVA) was used to test for the effect of UVR and logging treatment on Chl *a* accrual. Where a significant UVR x logging treatment interaction was detected, individual Bonferonni corrected RM-ANOVA's were performed for each logging treatment to determine where UVR had a significant effect of Chl *a* accrual. Multivariate analysis of variance (MANOVA) of dominate algal taxa was used to test for the effect of UVR and logging treatment on periphyton community composition on day 42 of the experiment. Repeated-measures multivariate analysis of variance (RM-MANOVA) of invertebrate abundance was used to test for treatment effects on invertebrate community composition. Significant treatment effects were further investigated using RM-ANOVA of individual taxa to determine which species had been effected. Finally, RM-ANOVA was used to test for the effect of logging and UVR on invertebrate diversity (*H'*). Post-hoc Student-Newman-Keuls tests where used to further investigate significant effects of logging treatment to determine at which sites differences occurred.

The low replication of treatments resulted in statistical tests having low power

(Appendix A). As a consequence, observations with *P*–values near α =0.05 are presented for discussion, bearing in mind the high probability of committing Type II errors.

All statistical analyses were performed on ln (n+1) transformed data when appropriate (Norris and Georges 1993, Zar 1996) using SPSS (v 6.1, 1995, SPSS Inc.) or SuperANOVA (v. 1.11, 1991, Abacus Concepts Inc.).

RESULTS

Physical and Chemical Data

Logging significantly increased solar radiation reaching the stream surface. Removal of the forest canopy resulted in an average 8.3 fold increase in mean daily PAR in the clear-cut over the unlogged reference. During the recorded periods, PAR irradiance averaged 3 E m^{-2} d^{-1} and ranged from 0.9 to 6 E m^{-2} d^{-1} in the unlogged reference and averaged 25 E m^{-2} d^{-1} and ranged between 4 and 44 E m^{-2} d^{-1} at the bottom of the clear-cut (Fig. 3.3a). Similarly, UVA and UVB fluxes were approximately 5.4 and 2.8 times greater respectively at the bottom of the clear-cut. Mean daily UVA irradiance was 123 kJ m^{-2} d^{-1} and 661 kJ m^{-2} d^{-1} in the unlogged reference and clear-cut respectively (Fig. 3.3b). UVB averaged 12 kJ m^{-2} d^{-1} in the reference and 33 kJ m^{-2} d^{-1} in the clear-cut (Fig. 3.3c). In the unlogged reference, UVA ranged from 25 to 253 kJ m^{-2} d^{-1} and UVB from 9 to 15 kJ m^{-2} d^{-1}. In the bottom of the clear-cut, UVA ranged from 75 to 1187 kJ m^{-2} d^{-1} and UVB from 13 to 52 kJ m^{-2} d^{-1}.

The concentration of DOC at each site influenced the proportion of incident solar radiation reaching the stream bottom. DOC averaged 6.2 mg C l^{-1} in the unlogged reference and 10.5 mg C l^{-1} at the bottom of the clear-cut (Table 3.2). In the unlogged reference, this resulted in an average 21% reduction in UVA and 44% reduction in UVB penetrating to 5 cm, and an average 39% and 75% reduction in UVA and UVB in the clear-cut (Fig. 3.4). The concentration of DOC was highest during increased spring

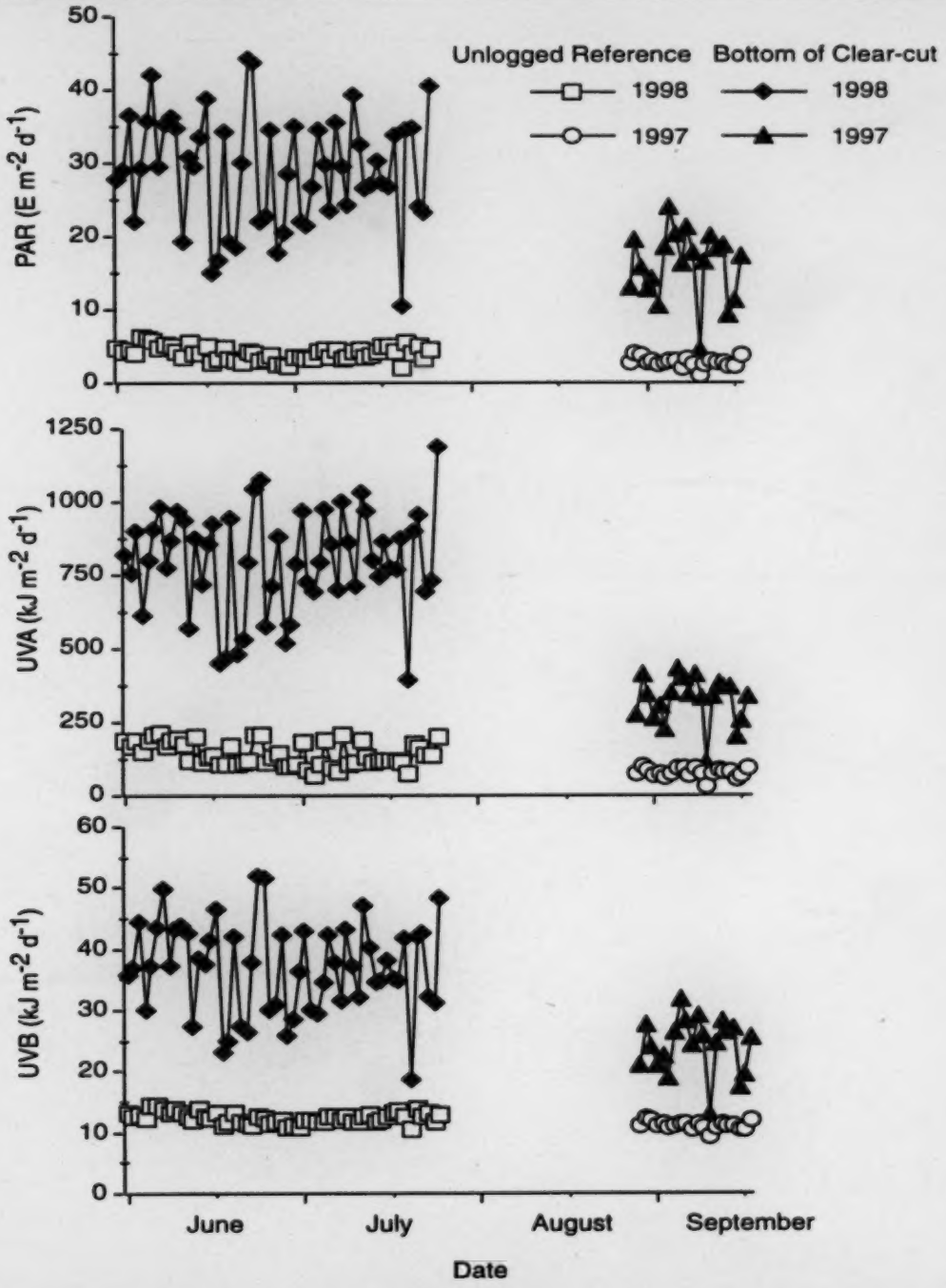

Figure 3.3: Solar radiation (PAR, UVA and UVB) in the unlogged reference and bottom clear-cut sites during the recorded periods of 1997 (mid August to mid September) and 1998 (June to mid July).

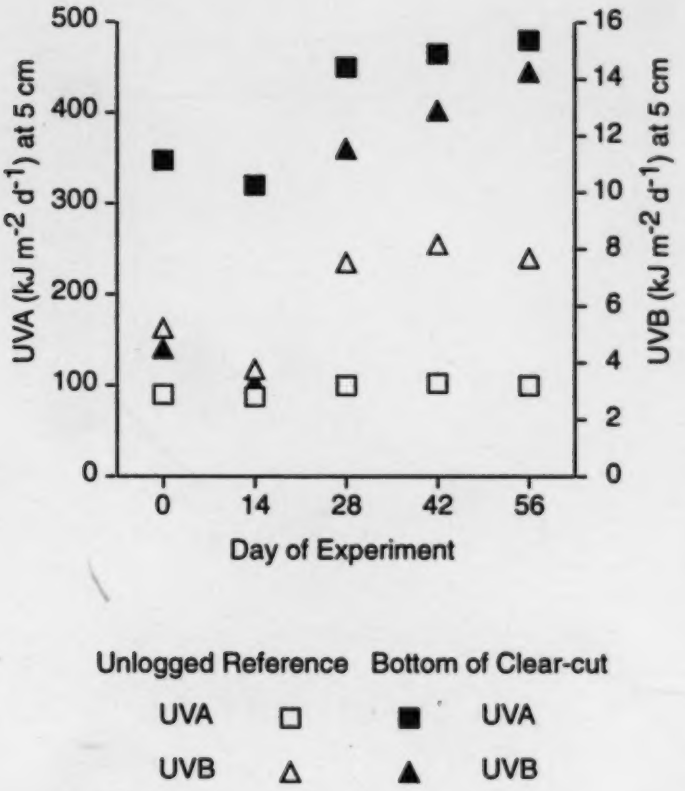

Figure 3.4: DOC adjusted mean daily UVA and UVB irradiance reaching to 5cm depth in the unlogged reference and clear-cut sites.

runoff, and declined during summer baseflow. While higher concentrations of DOC in the clear-cut greatly diminished the effect of logging in increasing biologically active UV radiation, average UVA and UVB remained higher in the clear-cut than in the unlogged reference.

Incident solar radiation was assumed to be nearly equal between the bottom clear-cut and top clear-cut sites. The sites were separated by 300m, had the same orientation and bank height, and the riparian canopy was not significantly different. Canopy closure measured with a spherical densiometer (Lemmon 1957) averaged 73.3% in the unlogged reference, 1.5% at the top of the clear-cut and 2.2% at the bottom of the clear-cut. DOC was not measured at the top of the clear-cut.

Stream temperature was significantly higher in the logged reach of Baptiste Creek. During the summer prior to logging, mean summer temperature was 6.3°C in both the unlogged reference and bottom clear-cut sites (Bruce MacDonald, Department of Fisheries and Oceans, unpublished data). During our experiment in the summer following logging, mean temperature was 8.1°C in the unlogged reference, 9.6°C at the top of the clear-cut, and 10.6°C at the bottom of the clear-cut (Fig. 3.5a) This resulted in total accumulated degree days being 395 in the unlogged reference, 489 at the top of the

Table 3.2: Select limnological variables for Baptiste Creek. Water samples were collected bi-weekly during the experimental period. Physical characteristics of the Baptiste watershed and details of logging treatment.

	Unlogged reference		Top of clear-cut		Bottom of clear-cut	
Variable	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
DOC (mg C l^{-1})	6.2	1.3	–	–	10.5	2.5
TDP (µg l^{-1})	7.4	1.2	–	–	16.7	5.1
Nitrate (µg l^{-1})	20.1	14.7	–	–	20.6	28.3
TDN (µg l^{-1})	223.6	39.1	–	–	317.7	125.6
Temperature (°C)	8.1	0.8	9.6	1.2	10.6	2.1
Degree days	395	–	489	–	565	–
pH	7.7	0.2	–	–	7.6	0.2
Alkalinity (µeq l^{-1})	88.2	20.7	–	–	74.0	8.0
Baseflow (cm^3 s^{-1})	20	–	27.5	–	36	
Depth (cm)	8.1	2.8	5.8	2.2	5.8	2.5

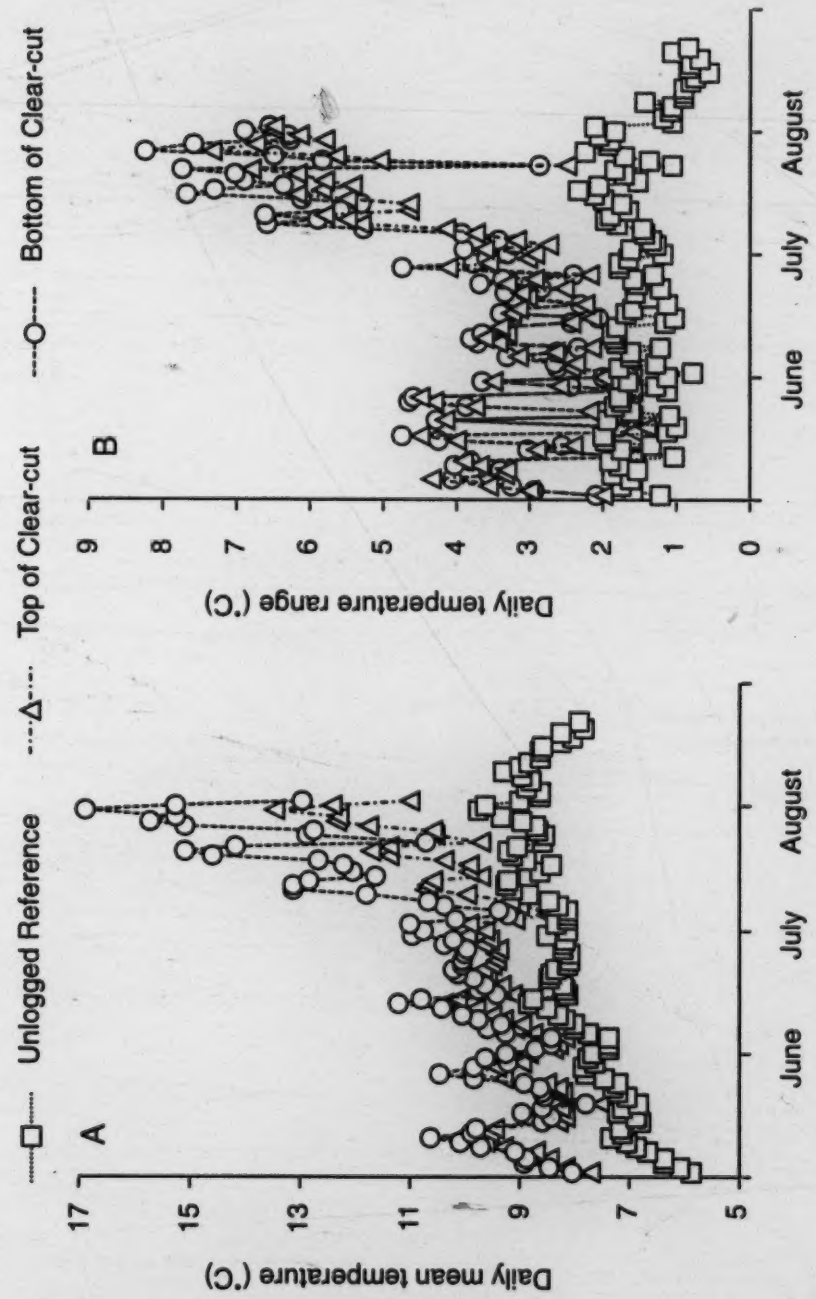

Figure 3.5: Daily mean temperature (A) and range in temperature (B) in Baptiste Creek at the unlogged reference, top clear-cut and bottom clear-cut sites.

clear-cut, and 565 at the bottom of the clear-cut (Table 3.2). Throughout the day, stream temperature fluctuated an average 1.5°C in the unlogged reference, 3.8°C at the top of the clear-cut, and 4.1°C at the bottom of the clear-cut (Fig. 3.5b).

Concentrations of inorganic nutrients were higher in the logged reach of Baptiste Creek than in the upstream reference. Mean total dissolved phosphorus was 7.4 $\mu g\ l^{-1}$ in the unlogged reference and 16.7 $\mu g\ l^{-1}$ in the bottom clear-cut (Table 3.2). Mean total dissolved nitrogen was 223.6 $\mu g\ l^{-1}$ in the unlogged reference and 317.7 $\mu g\ l^{-1}$ at the bottom of the clear-cut. The increase in TDN resulted from an increase in nitrogen species other than nitrate, which remained relatively constant at 20 $\mu g\ l^{-1}$ in the reference and 21 $\mu g\ l^{-1}$ in the clear-cut. pH was similarly neutral between the two sites, however, alkalinity dropped from 88.2 $\mu eq\ l^{-1}$ in the unlogged reach to 74.0 $\mu eq\ l^{-1}$ in the bottom of the clear-cut.

Chlorophyll a

RM-ANOVA of Chl *a* showed that logging along the stream resulted in significantly lower Chl *a* accrual ($P<0.001$, Table 3.3, Fig. 3.6). Over the course of the experiment, Chl *a* in the unlogged reference was on average 2.7 $\mu g\ cm^{-2}$ higher than the top of the clear-cut (SNK $P<0.05$) and 1.5 $\mu g\ cm^{-2}$ higher than the bottom of the clear-cut (SNK $P<0.05$). Chl *a* also varied within the clear-cut, although not significantly,

Table 3.3: Repeated-measures ANOVA results for the effects of ultraviolet radiation (UV) and logging treatment (Site) on log-transformed chlorophyll *a* values.

Source	df	*F*–statistic	*P*–value
UV	1	1.66	0.20
Site	2	46.45	< 0.001
UV x Site	2	4.26	0.021
Time	3	85.75	< 0.001
Time x UV	3	4.02	0.0090
Time x Site	6	5.52	< 0.001
Time x UV x Site	6	1.57	0.16

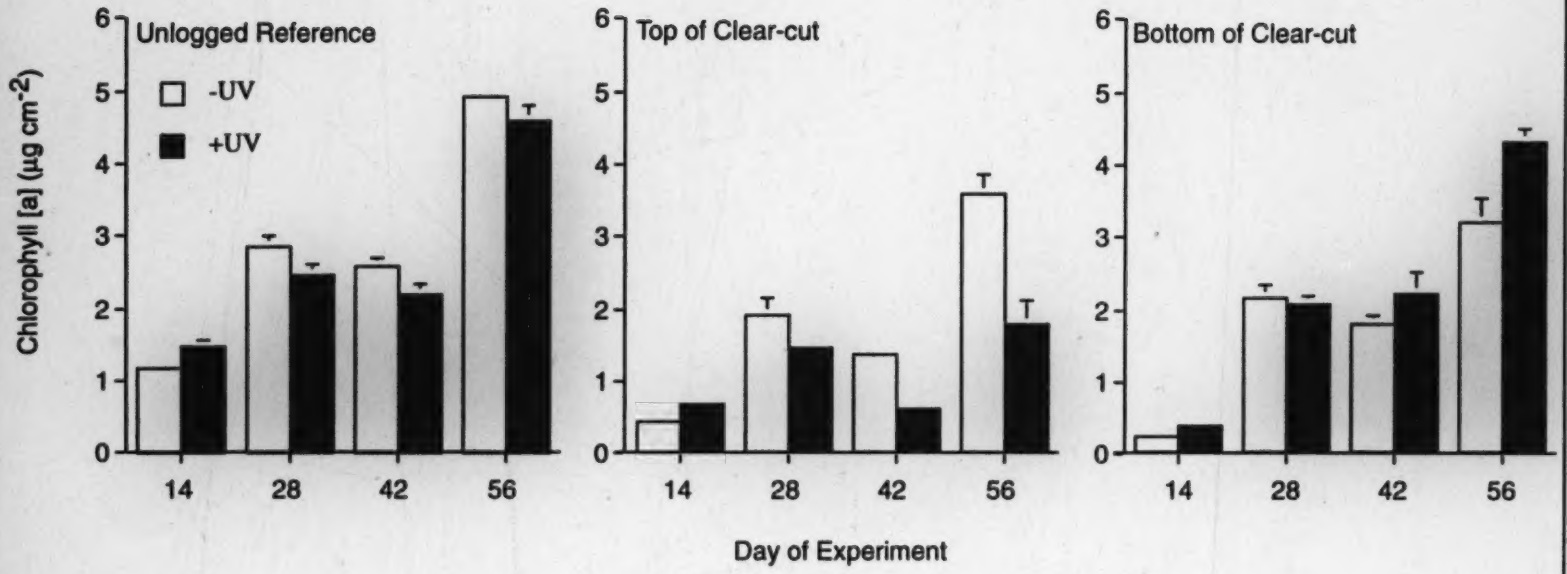

Figure 3.6: Chlorophyll *a* concentrations under UV shielded (white) and UV exposed (black) treatments in the unlogged reference, top of clear-cut and bottom of clear-cut sites. Error bars are ± standard error.

averaging 1.1 μg cm^{-2} lower at the top of the clear-cut than at the bottom (SNK $P>0.05$).

The effect of UV exposure on Chl *a* varied with logging treatment (UV x Site interaction, Table 3.3, Fig. 3.6). In the unlogged reference, there was no significant effect of UV, with only a small average difference of 0.2 μg cm^{-2} between UV exposed and UV shielded treatments (post-hoc RM-ANOVA $P=0.43$). However, at the top of the clear-cut, Chl *a* was significantly higher when shielded from UV, and was 1.8 μg cm^{-2} higher by the final sampling date ($P=0.0042$). This effect did not persist throughout the entire clear-cut; Chl *a* at the bottom of the clear-cut was only an average 0.4 μg cm^{-2} higher in the UV exposed treatment, compared to the UV shielded treatment ($P=0.27$).

Table 3.4: Day 42 mean species richness, diversity, and total fresh biomass for algal (>5% total biomass) exposed to (+UV) or shielded from (–UV) ultraviolet radiation in both the unlogged reference and clear-cut sites.

	Unlogged reference		Top of clear-cut		Bottom of clear-cut	
	+UV	–UV	+UV	–UV	+UV	–UV
N	4	4	2	2	2	2
Species richness	10.3	7.5	7.3	9.5	7.5	8.0
Diversity (*H'*)	2.1	1.1	1.1	0.69	1.6	2.0
Diatoms (μg cm^{-2})	**15.3**	**14.5**	**36.2**	**21.8**	**5.1**	**6.1**
Achnanthes minutissima	1.0	1.4	7.3	7.1	0.5	0.3
Cocconeis placentula	0.1	0.1	0	1.1	0.6	0.7
Craticula halophila	0	0	0	0.2	0.1	0.3
Cymbella descripta	0.1	0	0	0	0.5	0
Fragilaria ulna	0	0.1	0	0	0.3	0
Gomphonema parvulum	9.9	10.4	26.9	11.3	1.9	3.9
Meridion circulaire	0.4	0.5	0.6	1.2	0.8	0.1
Nitzschia sigmoidea	1.0	0.7	0	0	0	0
Rhopalodia gibba	0.8	0	0	0	0	0
Cryptophytes (μg cm^{-2})	**0.2**	**0**	**0.04**	**0**	**0**	**0**
Cyanobacteria (μg cm^{-2})	**0.03**	**0.2**	**0**	**0**	**0**	**0**
Chlorophytes (μg cm^{-2})	**0.004**	**0**	**0**	**0**	**0**	**0**

Algal Composition

Algal communities in Baptiste Creek were dominated by diatoms on day 42 of the experiment (Table 3.4). Total algal biomass was significantly affected by logging (ANOVA $P<0.001$), increasing at the top of the clear-cut (SNK $P<0.05$) but decreasing at the bottom of the clear-cut (SNK $P<0.05$). Algal biomass in the top of the clear-cut was on average 2 times higher than the unlogged reference, and 5 times higher than the bottom of the clear-cut. Algal biomass at the bottom of the clear-cut was 3 times lower than the unlogged reference.

Exposure to UV radiation did not affect total algal biomass in either the unlogged reference or bottom clear-cut sites. However, at the top of the clear-cut, exposure to UV resulted in 66% more total algal biomass (Table 3.4).

MANOVA of individual algal taxa comprising greater than 5% of the total biomass showed that algal community composition changed with logging ($P=0.004$, Table 3.5). Relative to the unlogged reference, the abundance and relative proportion of *Gomphonema parvulum* and *Achnanthes minutissima* significantly increased at the top of the clear-cut, and declined at the bottom of the clear-cut (SNK, $P<0.05$, Fig. 3.7). The abundance of other algal taxa did not change with logging.

Exposure to UV radiation affected algal communities differently in the three logging treatments (UV x Site interaction, $P=0.01$). Again, this was driven primarily by *G. parvulum*. In the unlogged reference, there was no significant difference is *G.*

Table 3.5: Results of MANOVA of the effects of solar ultraviolet radiation (UV) and logging treatment (Site) on algal community composition on day 42 of the experiment. Analysis was restricted to algal taxa >5% total biomass.

Source	df	*F*–statistic	*P*–values
UV	1	2.67	0.31
Site	2	10.09	0.0044
UV x Site	2	6.59	0.014

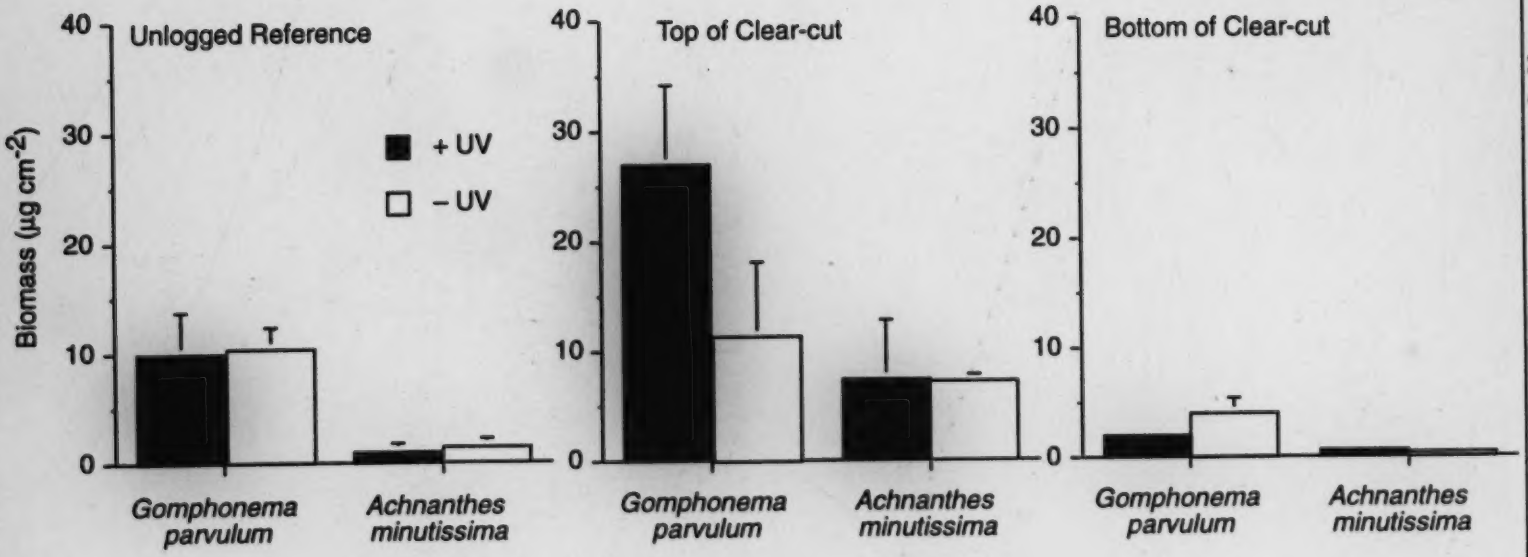

Figure 3.7: Fresh weight biomass of *Gomphonema parvulum* and *Achnanthes minutissima* under UV exposed (black) or UV shielded (white) treatments in the unlogged reference, top clear-cut and bottom clear-cut sites during week six (day 42) of the experiment. Error bars are ± standard error.

parvulum between UV treatments. However, in the top of the clear-cut, *G. parvulum* was 138% higher under UV exposed compared to UV shielded conditions. In contrast, at the bottom of the clear-cut, *G. parvulum* was 51% lower when exposed to UV (Fig. 3.7).

Invertebrate Community

Logging decreased invertebrate diversity (RM-ANOVA $P<0.001$; Fig. 3.8). Diversity in the bottom of the clear-cut was significantly lower than either the unlogged reference or the top of the clear-cut (SNK $P<0.05$). However, there was no significant difference in invertebrate diversity between the unlogged reference and the top of the clear-cut. Ultraviolet radiation did not significantly affect invertebrate diversity in any of the logging treatments.

Total invertebrate density at the bottom of the clear-cut was significantly higher than both the unlogged reference and top clear-cut sites (RM-ANOVA $P=0.0045$; SNK $P<0.05$; Fig. 3.9a). The increase was driven by an explosion of Diptera, primarily chironomids, in the bottom of the clear-cut (RM-MANOVA $P=0.0036$; Table 3.6; Fig. 3.9b). During the first 42 days of the experiment, chironomid density averaged approximately 350% higher in the bottom of the clear-cut than either the unlogged reference or top of the clear-cut. By day 56 however, chironomid density had declined in the bottom of the clear-cut, and was not different from the other logging treatments.

Table 3.6: Results of RM-MANOVA of the effects of ultraviolet radiation (UV) and logging treatment (Site) on density of Diptera, Plecoptera and Ephemeroptera.

Source	df	Diptera		Plecoptera		Ephemeroptera	
		F	*P*	*F*	*P*	*F*	*P*
UV	1	0.26	0.78	1.12	0.42	0.65	0.60
Site	2	5.17	0.0036	10.76	<0.001	1.53	0.23
UV x Site	2	0.43	0.78	0.88	0.56	1.20	0.35
Time	3	2.37	0.041	6.25	<0.001	6.12	<0.001
Time x UV	3	0.94	0.47	1.07	0.40	1.00	0.45
Time x Site	6	1.58	0.12	2.11	0.0058	1.11	0.36
Time x UV x Site	6	0.87	0.58	1.95	0.012	0.59	0.90

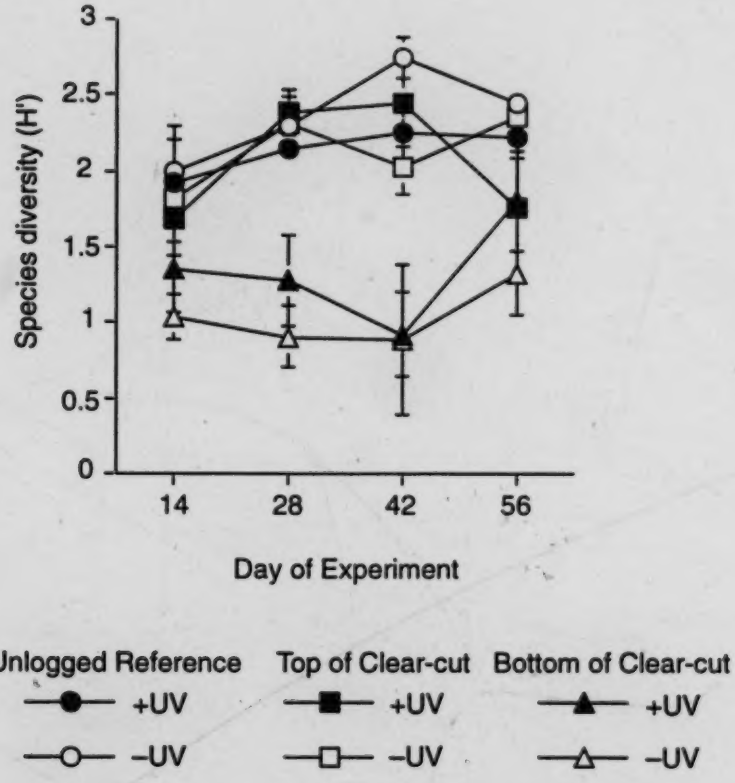

Figure 3.8: Species diversity (H') of the invertebrate community under UV exposed (black) and UV shielded (white) treatments in the unlogged reference (circle), top clear-cut (square), and bottom clear-cut (triangle) sites. Error bars are ± standard error.

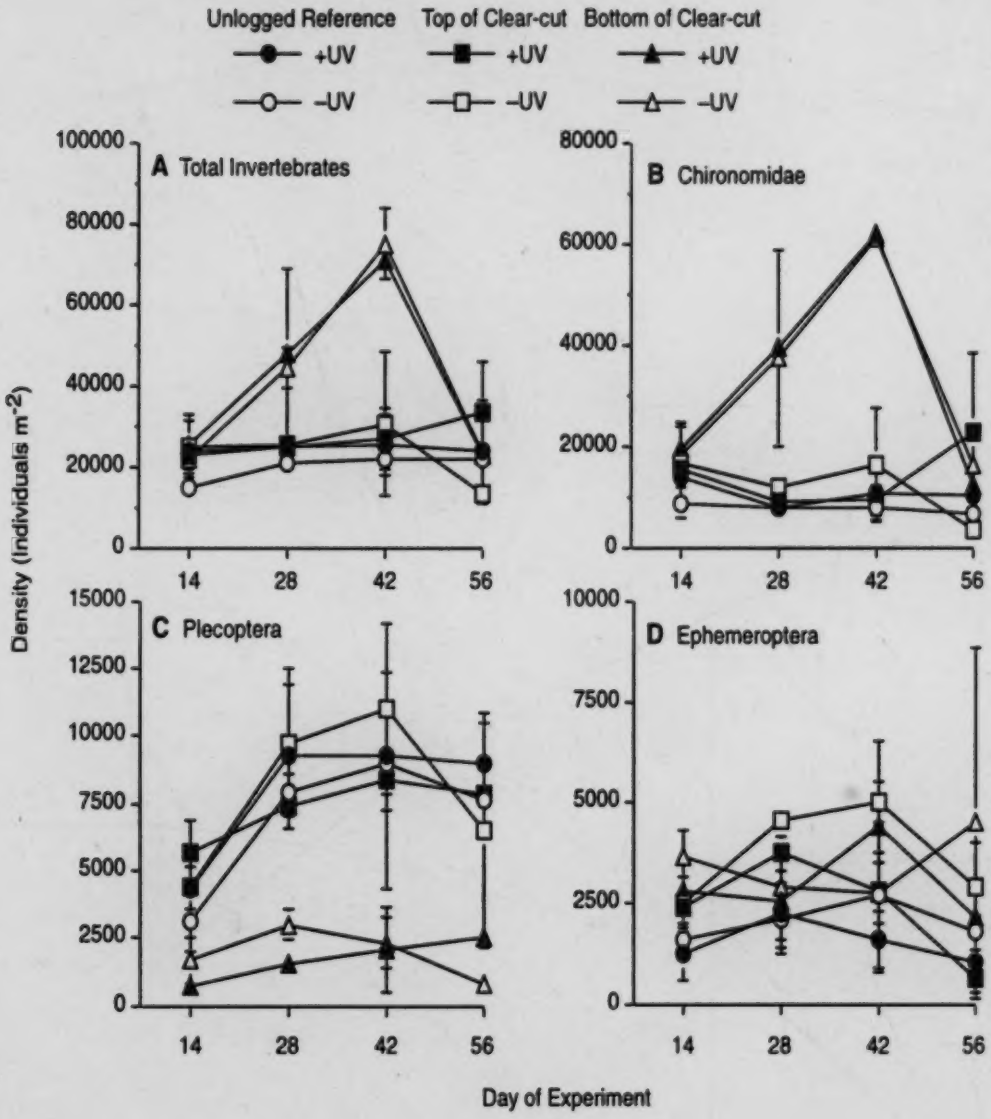

Figure 3.9: Total invertebrate (A), Chironomidae (B), Plecoptera (C), and Ephemeroptera (D) densities between UV exposed (black) and UV shielded (white) treatments in the unlogged reference (circle), top clear-cut (square), and bottom clear-cut (triangle) sites. Error bars are ± standard error.

Throughout the entire experiment, total invertebrate and chironomid densities at the top of the clear-cut were not significantly different than the unlogged reference.

While chironomids increased at the bottom of the clear-cut, Plecoptera decreased (RM-MANOVA $P<0.001$; Table 3.6; Fig. 3.9c). Total stonefly density averaged 68% lower in the bottom of the clear-cut than both the unlogged reference and top clear-cut. Stonefly response to logging was driven by 2 taxa that declined at the bottom of the clear-cut (RM-ANOVA Leuctridae $P<0.001$; Chloroperlidae $P=0.0014$, Fig. 3.10 a,b) and one species that increased at the bottom of the clear-cut (*Zapada spp.* $P<0.001$; Fig. 3.10d). Again, there was no significant difference in Plecoptera density between the top of the clear-cut and the unlogged reference. Finally, total Ephemeroptera density was not significantly affected by any logging treatment (RM-MANOVA $P=0.23$; Fig. 3.9d).

Despite no significant UV x Site interaction in any of the invertebrate groups (Table 3.6), there were different effects of UV exposure in the different sections of Baptiste Creek. While the effect of logging was strongest at the bottom of the clear-cut, invertebrates there did not respond to UV exposure (Fig. 3.9). Similarly, there was no clear difference in invertebrate density between UV exposed and UV shielded treatments in the unlogged reference. However, at the top of the clear-cut, mayfly density averaged 50% greater in UV protected environments, a difference that increased steadily over the course of the experiment (Fig. 3.9d). Similarly, during the first 42 days of the experiment, chironomid and total stonefly densities at the top of the clear-cut were consistently higher when shielded from UV (Fig. 3.9b,c).

DISCUSSION

Effects of logging on the stream environment

In the unlogged reach, Baptiste Creek resembled a typical small boreal stream. The thick riparian forest shaded the stream from incoming solar radiation, keeping

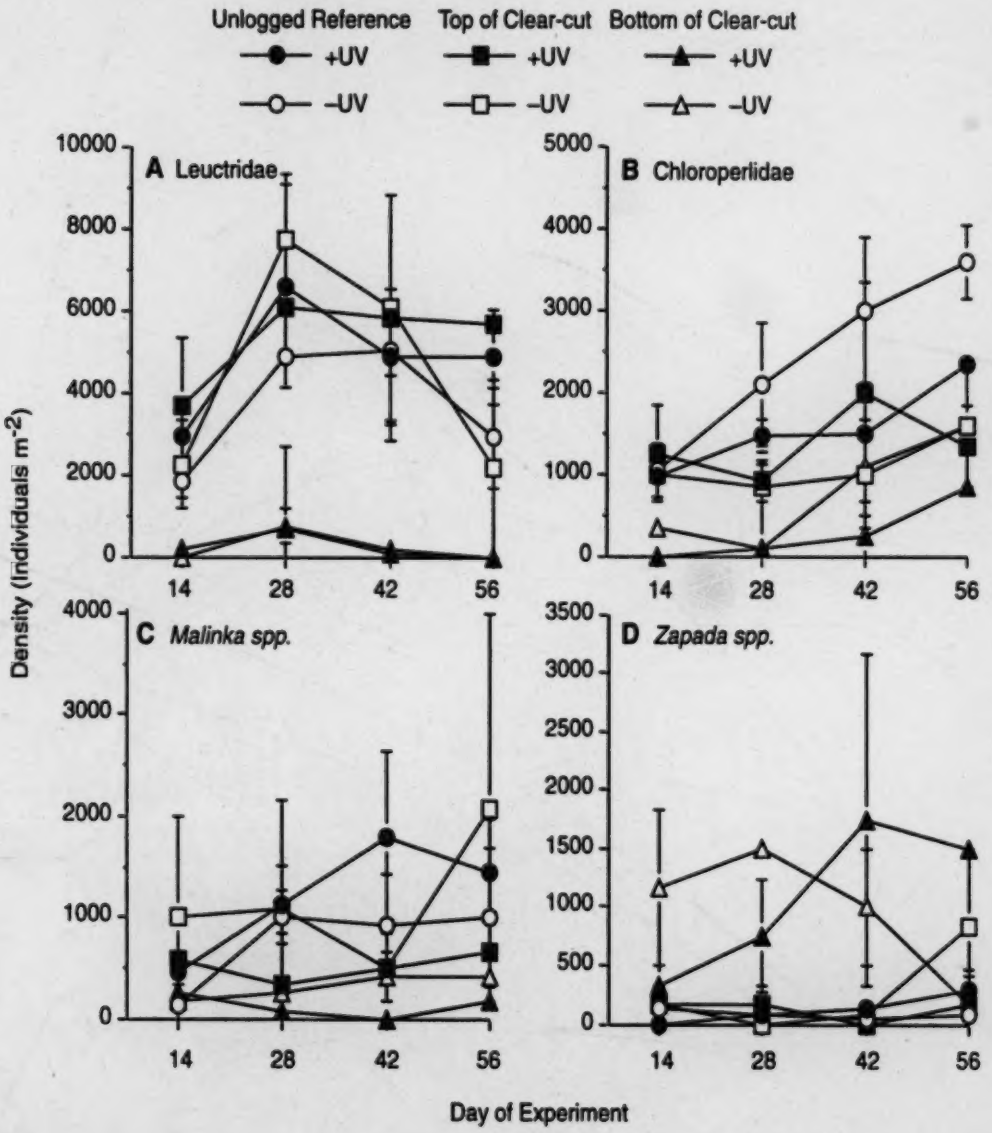

Figure 3.10: Density of stonefly (Plecoptera) taxa in both the UV exposed (black) and UV shielded (white) treatments in the unlogged reference (circle), top clear-cut (square) and bottom clear-cut (triangle) sites. Error bars are ± standard error.

incident PAR and UV radiation fluxes relatively low. In addition, moderate concentrations of DOC resulted in the attenuation of approximately half of the incident UV radiation within the first 5 cm of the water column. The stream was also characterized by low, stable water temperatures, and relatively low concentrations of dissolved nutrients.

Our observations in the unlogged reference indicate that riparian forests highly influence small streams. Previous research has shown that small forested streams typically receive only 1 to 3% of total available solar radiation (Naiman *et al.* 1992, Chen *et al.* 1999). While several factors, including aspect, valley incision, and catchment topography can all influence the amount of light reaching a stream, riparian vegetation is the primary controlling factor which determines how much light gets through (Naiman *et al.* 1992). Shading of incoming solar radiation by riparian forests also maintains relatively low daily mean temperatures. Shading dampens diurnal temperature increases, and coupled with an insulating effect that prevents nocturnal temperature declines, riparian forests also stablize thermal environment, with only small oscillations in daily temperature (Bescheta *et al.* 1987). Finally, riparian forests strongly regulate the amount of nitrogen and phosphorus reaching streams from upland areas (Karr and Schlosser 1978, Pinay *et al.* 1990). Riparian forests take up nutrients from the soil, promote denitrification, and modify the chemical composition and availability of carbon and phosphorus.

Clear-cutting of the Baptiste Watershed, and in particular, alteration of the riparian zone, led to significant increases in light exposure, water temperature, and nutrient loads. However, we observed different effects of logging at the top and bottom of the clear-cut. Removal of the riparian canopy resulted in an instantaneous increase in solar exposure and thermal variability that was consistent at both the top and bottom of the clear-cut. However, the effect of logging on daily mean temperature, DOC concentration, and nutrient concentrations accumulated with distance downstream from the forest/clear-cut

edge. Daily mean temperature at the top of the clear-cut, 250 m from the forest/clear-cut edge, was 1.5°C higher than the unlogged reference. Six hundred meters into the clear-cut, daily mean temperature was 2.5°C greater than the unlogged reference. The increase in DOC and nutrients that we observed at the bottom of the clear-cut was likely a function of the proportion of the catchment logged, and of the length of channel harvested, at any given point in the stream. As a result, DOC and nutrients at the top of the clear-cut were probably higher than in the unlogged reference, but lower than at the bottom of the clear-cut.

This combination of instantaneous and cumulative effects on light exposure, stream temperature, and nutrient concentrations resulted in the stream being characterized at the top of the clear-cut by high incident light exposure, a relatively small increase in mean daily temperature, an increase in daily thermal variation, and a small increase in nutrient concentrations. In addition, relatively low concentrations of DOC resulted in a greater proportion of incident UV radiation reaching the stream bottom. At the bottom of the clear-cut, the stream was characterized by high solar radiation, high mean and daily range in temperatures, and relatively high nutrient concentrations. Significant increases in DOC meant that a smaller fraction of the incident UV radiation reached the benthic community.

Despite the ameliorating effect of increased DOC at the bottom of the clear-cut, exposure of the benthic community to UV-B still increased 200% over that in the unlogged reach of the stream. In addition, the increase in DOC with logging was probably short lived. Meyer and Tate (1983) observed that after an initial pulse of DOC following logging, long-term DOC export from a clear-cut watershed declined.

No studies have examined the gradient of effects logging creates in streams as they flow through clear-cuts. Most studies either examine single sites before and after logging (e.g., Hartman and Scrivener 1990, Garman and Moring 1991) or compare single sites between clear-cut and reference watersheds (e.g., Hetrick *et al.* 1998a,b). The

effects of logging these studies report may therefore be incomplete, being highly dependent upon where within the clear-cut samples are collected. The results of our experiment clearly demonstrate that while some environmental changes, such as increased light exposure, may occur instantaneously and consistently throughout clear-cuts, other effects, such as increased temperature, may increase in magnitude with distance into the cut block.

We observed significant effects of logging despite the retention of all non-merchantable trees within the 20 m wide Riparian Management Zone (RMZ). In fact, the increase in solar exposure we observed in Baptiste Creek was similar to other studies where no riparian buffer at all was left along the stream (Brosofske *et al.* 1997, Chen *et al.* 1999). Similarly, the increase in temperature and nutrients at the bottom of the clear-cut were of the same magnitude as in studies where little or no riparian forest was left intact along the stream channel (Hobbie and Likens 1973, Lynch *et al.* 1984, Hetrick *et al.* 1998a). The inability of the RMZ to ameliorate the effects of logging within Baptiste Creek was likely due to the retained trees small size and thin spacing. There were simply not enough trees left standing to prevent significant alteration of the stream. The removal of merchantable trees all the way to the stream bank resulted in complete destruction of the forest understory (Plate 4.1). In addition to eliminating the effect shrubs may have had on the uptake and alteration of nutrients in soils adjacent to the stream, this also deleted any compensatory shading shrubs may have provided upon removal of the forest canopy.

We did not measure several environmental factors in Baptiste Creek that have been observed to change with logging elsewhere. For example, in a comprehensive, 17 year study of Carnation Creek, Hartman and Scrivener (1990) described how logging also changed stream channel structure, increased amounts of large woody debris, increased sediment transport, and increased bedload movement. While we did not measure these factors, we believe most of them to be of little significance in our experiment. We

examined the effect of logging in Baptiste Creek immediately following harvest, with a focus on benthic algal and invertebrate communities. Annual changes in channel morphology in Carnation Creek were accelerated with logging (Hartman and Scrivener 1990), but such changes were apparent over years, not within one summer. Similarly, increases in the amounts of large woody debris are significant for their role in channel and streambed stability, and in providing habitat for fish species, but are not necessarily important the summer after logging in a fishless stream. Bedload transport in Carnation Creek increased after logging, but significant bedload movement only occurred during freshets (Hartman and Scrivener 1990). Our experiment in Baptiste Creek was conducted after spring runoff, on clean uncolonized substrate. As a result, any change in bedload movement with logging would not have directly impacted our study.

Increased suspended sediment transport with logging, however, may have had significant consequences for our experiment. High suspended sediment concentrations during storms in clear-cut watersheds have been observed in several studies (Lisle 1982, Garman and Moring 1990, Hartman and Scrivener 1990, Heede 1991). These periodic episodes of high sediment flows can scour periphyton from cobbles (Biggs 1996, Peterson 1996) and set invertebrates adrift (Rae 1987). During our experiment, there were 5 storms (>10 mm precipitation) that may have resulted in scouring events within the clear-cut. Unfortunately, we did not measure suspended sediments during these periods and therefore do not know what effect increased sediment loads had on our experiment.

The benthic ecosystem in the unlogged reference

Algal and invertebrate communities in the unlogged reach of Baptiste Creek were typical of a light-limited, headwater boreal stream. While benthic Chl *a* in streams can span four orders of magnitude, the range of Chl *a* in unenriched, forested catchments is typically 5 to 30 $\mu g\ cm^{-2}$ (Biggs 1996). Chlorophyll *a* in the unlogged reference of

Baptiste Creek increased from just over 1 μg cm^{-2} after 14 days of colonization, to 5 μg cm^{-2} at the end of the experiment.

The algal community in the unlogged reference consisted almost entirely of diatoms. Only a small fraction of algal species counted on day 42 of the experiment were cryptophytes, cyanobacteria, or chlorophytes (Table 3.4). Instead, the community was dominated by *Gomphonema parvulum*, a medium sized (300 μm^3 biovolume [Lowe and Pan 1996]) diatom that grows on mucilaginous stalks (Burkholder *et al.* 1990), and *Achnanthes minutissima*, a small (70 μm^3 biovolume [Bothwell *et al.* 1993]) diatom that grows tightly adhered to the substrate (Biggs 1996).

The benthic algal community in the unlogged reference was likely light limited. Steinman *et al.* (1989) predicted that diatoms would dominate moderately grazed benthic algal communities at low light conditions, below 50 μmol m^{-2} s^{-1}. Light intensity in the unlogged reach averaged 35 μmol m^{-2} s^{-1}. In addition, the growth of *A. minutissima* indicted that periphyton were not nutrient limited. Several studies have observed that *A. minutissima* prefers nitrogen and/or phosphorus enriched environments (McCormick and Stevenson 1989, Stevenson *et al.* 1991, Peterson and Grimm 1992).

The composition of the benthic invertebrate community was also reflective of a healthy headwater stream. The diversity of invertebrate species in the unlogged reference was comparable to studies in other undisturbed streams (Newbold *et al.* 1980, Carlson *et al.* 1990). This was a result more of species evenness, than of richness. The evenness of the invertebrate community is reflected by the ratio of EPT abundance (Ephemeroptera, Plecoptera, and Tricoptera) to Chironomidae abundance. A community dominated by chironomids is generally viewed to be under environmental stress (Resh and Jackson 1993) and consequently would have lower diversity. In the unlogged reference, the ratio of EPT to Chironomidae was just over 1 to 1.

The effect of logging at the top of the clear-cut

Algae at the top of the clear-cut responded to increased light by decreasing Chl *a*, but increasing biomass, relative to the unlogged reference. The increase in algal biomass was driven by an increase in the abundance of *G. paravulum* and *A. minutissima* (Table 3.4). This is in contrast to previous studies, where an increase in Chl *a* was accompanied by a taxonomic shift from diatoms to chlorophytes and cyanobacteria following logging (Stockner and Shortreed 1976, Lowe *et al.* 1986, Hartman and Scrivener 1990). Instead, the algal community at the top of the clear-cut simply responded to increased light by increasing the abundance of the two major diatom species.

The paradoxical decrease in Chl *a* with increased algal biomass may have occurred for several reasons. First, the increase in algal biomass was due to an increase in diatoms, which do not contain a high amount of Chl *a*. Chlorophytes and cyanobacteria, which do contain high amounts of Chl *a*, were present in the unlogged reference, but absent at the top of the clear-cut (Table 3.4). This taxonomic change alone may have resulted in lower composite Chl *a* concentrations at the top of the clear-cut. Second, photoacclimation of algae in the unlogged reference may have resulted in more Chl *a* per algal cell. This is a common response of all types of algae to low ambient light intensities (Falkowski and LaRoche 1991) and is characterized in part by increases in the number and density of thylakoid membranes (Berner *et al.* 1989) and by changes in pigment content and composition (Falkowski and LaRoche 1991, Hill *et al.* 1995). As a result, there may have been a decline in the amount of Chl *a* per algal cell at the top of the clear-cut, but not necessarily a decline in algal density.

Algae at the top of the clear-cut also responded to UV radiation. Chl *a* was significantly higher when shielded from UV radiation, yet algal biomass was significantly higher when exposed to UV radiation. Again, Chl *a* and algal biomass may not have correlated well for several reasons. For example, the amount of Chl *a* produced by periphyton may decrease when exposed to high UV radiation. Vincent *et al.* (1984)

found that exposure to UV light intensified the photoinhibitory response of phytoplankton. In addition, exposure to UV radiation may decrease Chl *a* per cell as algae devote more cellular resources to the production of protective accessory pigments (Falkowski and LaRoche 1991, Karentz *et al.* 1994). For example, Donahue (2000) found that the protective pigment scytonemin accounted for up to 90% of the total pigment compliment in epilithon exposed to UV radiation in shallow littoral communities of lakes. Given a tradeoff between producing high amounts of Chl *a* and suffering cellular damage, or producing protective pigments at the expense of Chl *a*, algae may be highly selected for towards the latter. This may be especially true in shallow, attached communities where lack of physical refugia result in prolonged exposure to high solar radiation. This may have contributed to low Chl *a* in algae exposed to UV radiation at the top of the clear-cut, even though biomass was high.

The effectiveness of Chl *a* as an estimate for algal biomass is tenuous at best and probably highly misleading when comparing algal communities incubated under different light conditions. It is possible that individual algal cells will respond physiologically to local light conditions, independent of a change in the density or biomass of the community. As a result, cell counts on day 42 of the experiment were the best indicator of the amount of algae present in the stream. In summary, the algal community at the top of the clear-cut responded to logging and increased light by increasing biomass. This increase was highest when algae were exposed to UV, and lowest when algae were shielded from UV. We discuss below what role indirect trophic interactions (Bothwell *et al.* 1994) may have played in increasing algal biomass despite being exposure to UV radiation.

There was no significant difference in total invertebrate abundance between the top of the clear-cut and the unlogged reference. In addition, there was no change in the taxonomic composition of the invertebrate community, or in the density of individual

taxa, between the two sites. This suggests that invertebrates did not respond to increased light intensity, a moderate increase in temperature, or the observed increase in algal biomass. This is in contrast to other studies which have observed bottom-up control of invertebrate production in logged streams (Newbold *et al.* 1980, Carlson *et al.* 1990, Hetrick *et al.* 1998b). For example, Newbold *et al.* (1980) concluded that invertebrate density in clear-cut streams increased as a result of increased primary productivity. Similarly, Hetrick *et al.* (1998b) concluded that benthic invertebrate densities and biomass were greater in open- than in closed-canopy sections of a small creek because of the greater biomass of periphyton in the open section, which in turn coincided with increased light intensity (Hetrick *et al.* 1998a). However, other factors associated with logging, such as increased water temperature, may also increase invertebrate abundance in clear-cut streams. Both Newbold *et al.* (1980) and Hetrick *et al.* (1998b) also observed increased stream temperature with canopy removal. It may be that a combination of these factors caused increased invertebrate abundance, and that increased algal biomass alone, as observed at the top of the clear-cut, may be insufficient to induce a response by invertebrates. This hypothesis is supported by our observation of increased invertebrate abundance at the bottom of the clear-cut, where logging resulted in a greater increase in stream temperature.

In addition, invertebrates in the UV exposed treatment may not have responded to increased algal productivity because the negative effects of UV radiation balanced the positive effects of increased food availability. While not statistically significant[†], mayfly abundance averaged 50% greater when shielded from UV radiation. In addition, during the first 42 days of the experiment, densities of chironomids and stoneflies were consistently higher in the –UV treatment. Significant direct negative effects of UV

[†] As mentioned in the statistical methods and results sections, a lack of statistical power stemming from low replication may have resulted in these differences not being statistically significant (Appendix A). However, we present this discussion as a possible interpretation of our results in the event that our observations, while not statistically significant, were ecologically significant (Chiplonkar and Prayag 1997, Kilgour *et al.* 1998).

radiation on aquatic invertebrates have been observed extensively (Bothwell *et al.* 1994, Kiffney *et al.* 1997, Vinebrooke and Leavitt 1999). A strong effect on invertebrates may have lead to a top-down "solar cascade" (Williamson 1995) occurring at the top of the clear-cut. A response by invertebrates to UV exposure may have led to decreased grazing intensity and the increased periphyton biomass we observed in the +UV treatment. Bothwell *et al.* (1994) observed such an interaction in small artificial stream flumes: a strong negative effect of UV radiation on invertebrate grazers resulted in increased periphyton accumulation, despite the direct negative effects of UV on periphyton.

The effect of logging at the bottom of the clear-cut

Despite significant increases in light exposure, temperature, and dissolved nutrients, Chl *a* and algal biomass at the bottom of the clear-cut were significantly lower than in the unlogged reference and at the top of the clear-cut. This was likely a result of increased chironomid abundance, and consequently, increased grazing intensity, at the bottom of the clear-cut. It seems likely that primary productivity increased at the bottom of the clear-cut, but did not translate into higher standing crops of algae, as we observed at the top of the clear-cut, due to the increased number of grazers. A similar result was observed in logged streams of Northern California: invertebrate density increased, while algal biomass and Chl *a* remained unchanged despite increases in light availability and nutrient concentrations (Newbold *et al.* 1980). Stevenson (1997) predicted that resource enrichment would result in increased algal biomass only if the rate of accumulation exceeded the rate of grazing.

The invertebrate community at the bottom of the clear-cut was significantly different from both the unlogged reference and top clear-cut sites. Chironomid density increased nearly three fold, while the abundance of most stonefly and mayfly species declined. These results suggest that the response of invertebrates to logging was not driven by increases in PAR and algal biomass alone, as concluded by other investigators

(Newbold *et al.* 1980, Hetrick *et al.* 1998b). Instead, we believe that changes in the invertebrate community were likely also a result of increased temperature. Temperature is a major factor in the ecology and evolution of aquatic insects (Ward 1982, Vinson and Hawkins 1998). Higher temperatures may increase growth rates (Ward 1982), resulting in more individuals present being retained during sampling. Temperature also influences an organism's metabolism, affecting the amount of resources required for daily activity and reproduction. In addition, a species temperature preference influences the ability of an organisms to successfully compete, thus influencing community composition and abundance (Naiman *et al.* 1992). Finally, invertebrates have specific requirements for the number of degree days necessary for egg development, molting, reproduction, and emergence, all of which affect the abundance of different species and the composition of the overall community (Sweeney and Vannote 1978). In addition to the direct effects of temperature on invertebrates, water temperature also influences water viscosity, the concentration of dissolved oxygen, and bacterial decomposition, which may also indirectly affect invertebrate communities. We believe that the increase in temperature observed at the bottom of the clear-cut was a necessary prerequisite, along with increases in primary production, for the observed change in invertebrate community composition, and the increase in chironomid abundance.

In contrast to the top of the clear-cut, neither the algal or invertebrate community at the bottom of the clear-cut responded to the presence or absence of UV radiation. There are at least two possible explanations for the different response to UV at the 2 sites. First, the concentration of DOC at the bottom of the clear-cut may have been high enough to shield communities from UV radiation, while at the top of the clear-cut, high doses of UV still penetrated to the stream bottom. Vinebrooke and Leavitt (1998) found DOC concentrations of 4 mg C l^{-1} significantly offset the response of littoral communities to UV in 1.2 meter deep enclosures in an alpine lake. Another study on shallow artificial streams (7 cm depth) found that DOC concentrations of 5 mg C l^{-1} effectively protected

the benthic community from UVR exposure (David Kelly, University of Alberta, unpublished data). Higher concentrations of DOC are needed to attenuate UV in shallow aquatic ecosystems. Dissolved organic carbon averaged 6.2 mg C l^{-1} in the unlogged reference and 10.5 mg C l^{-1} at the bottom of the clear-cut (Table 3.2), suggesting that DOC was high enough to attenuate UV at the bottom of the clear-cut, but may not have been high enough to absorb increased incident UV at the top of the clear-cut.

Secondly, the cumulative effects of logging on the stream environment at the bottom of the clear-cut may have overshadowed the singular effect of increased UV radiation. Thermal stress (Lamberti and Resh 1983, 1985, DeNicola 1996) and nutrient enrichment (Borchardt 1996, Stevenson 1997) alone can cause large changes in algal and invertebrate assemblages. These stressors were present in both UV treatments at the bottom of the clear-cut and may have eliminated UV sensitive species, despite the presence of a UV shielded environment. As a consequence, no response to UV shielding was detected.

Conclusions

Clear-cut logging in Baptiste Creek led to significant increases in light exposure, stream temperature, and concentrations of dissolved nutrients. In addition to increasing PAR, the results of our experiment clearly demonstrate that removal of the forest canopy also increased the exposure of the benthic community to UV radiation.

Our experiment demonstrates that the effect of logging was not consistent throughout the entire cut-block. Logging resulted in an instantaneous increase in some variables, such as light exposure, while effects on other variables, such as stream temperature, increased with distance downstream of the forest/clear-cut edge. This result suggests that the size of the cut-block, and the length of channel harvested, might be extremely important in determining the overall effect of clear-cut logging on streams.

In addition to the size of the cut-block, other characteristics of the logging

operation will influence what impact clear-cut logging may have on streams. The size and character of the buffer strip left alongside the stream channel may significantly mitigate the impact of logging (Castelle *et al.* 1994, Chen *et al.* 1999). For example, Newbold *et al.* (1980) recommended that complete buffer strips of 30 m would prevent significant effects on a wide range of abiotic and biotic factors. Our results suggest that a 20 m buffer strip comprised only of non-merchantable timber is insufficient to protect small headwater streams from the effects of clear-cut logging. In addition, the number of stream crossings within the cut-block, the method of logging employed (machine or hand felled), and whether or not trees are felled and yarded across the stream channel may also influence the final effect of logging on streams.

The characteristics of the stream and watershed are likely just as important in determining the effects of logging, as the nature of the logging operation itself. Channel characteristics which may be important include width, depth, and volume. For example, riparian vegetation has less influence on wider streams and rivers (Naiman *et al.* 1992), and benthic communities in deeper streams enjoy greater attenuation of UV by the water column. In addition, larger volume streams will have increasingly greater thermal inertia, and will require greater inputs of energy per degree increase in temperature. Characteristics of the watershed may also be important. The aspect of the watershed, particularly in higher latitude areas, will affect the number of hours a channel is exposed to direct sunlight each day. Similarly, the slope of the catchment, and particularly the slope of the hillside immediately adjacent to the stream channel, will affect the exposure of the channel to solar radiation, runoff from the catchment, and the severity of soil erosion and sediment inputs. For example, streams at the bottom of steep gullies may not experience increases in solar exposure with riparian logging, although they may be more susceptible to high erosion and increased suspended sediments. Finally, the chemical properties of the water may be important in determining the effect of logging. For example, streams already nutrient rich will likely not respond to an increase in nitrogen

or phosphorus with logging. Also, the natural concentration of DOC may affect the proportion of incident UV radiation that reaches to ecologically significant depths.

Because the effects of logging on the stream environment differed within the clear-cut, so too did its effects on the biological community. In our experiment, large changes in both the invertebrate and algal communities did not occur until lower down in the clear-cut. Obviously, streams represent a continuum, and disturbances in the watershed may not be observed immediately. Our results suggest that the biological effects of logging within a cut-block accumulate with distance downstream of the forest/ clear-cut edge. This observation may have significant implications for other studies of the effects of logging on streams, for results depend on where within the cut-block studies are conducted.

At the top of the clear-cut, exposure to UV appeared to have a significant effect on the stream ecosystem, while at the bottom of the clear-cut, UV had no observable effect. The removal of the forest canopy along streams, and the resulting increase in solar radiation, may therefore not automatically result in a response of the biotic community to UV radiation. Organisms are continually responding to an infinite number of niche dimensions, and the relative importance of UV radiation will therefore depend on the amount of UV individuals are exposed to, plus the relative severity of other environmental factors.

Finally, our experiment was carried out in the summer immediately following logging. It is expected that the response of the biological community to logging and UV radiation will change as the forest regenerates and DOC levels drops (Meyer and Tate 1983). More research is needed to assess the long term implications of logging, and the resulting increase in UV radiation, on stream ecosystems.

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Appendix A: Power analysis of factorial univariate repeated measures ANOVA tests at α=0.05. Value displayed is the probability (%) of not committing a type II error: not rejecting the null hypothesis when the null hypothesis is incorrect.

		Diptera			Plecoptera			Ephemeroptera		
Source	Chl a	Chironomidae	Simuliidae	Leuctridae	Malinka	Zapada	Chloroperlidae	Heptageniidae	Ameletidae	Baetidae
UV	24	6	5	8	14	6	6	5	8	10
Site	100	99	17	100	34	100	98	40	14	53
UV x Site	71	13	11	18	6	5	35	7	39	11
Time	100	63	66	99	50	20	100	44	89	100
Time x UV	84	38	11	29	16	8	15	14	23	27
Time x Site	100	89	22	51	53	48	76	19	17	63
Time x UV x Site	59	41	14	64	33	89	39	13	32	15

Chapter 4: General Conclusions

The effect of UV on freshwater ecosystems

Research on the effects of ultraviolet (UV) radiation on freshwater systems has progressed from the organism and sub-organism level to include multiple species interactions and responses of whole communities and ecosystems. Along with this move to include multiple levels of organization has come the realization that the impact of UV radiation is going to be complex rather than simple (Bothwell *et al.* 1994, Williamson 1995). Individuals, populations, and species at different trophic levels are going to vary in their sensitivity to UV, resulting in unpredictable changes at the ecosystem level (Bothwell *et al.* 1994, Karentz *et al.* 1994). In addition, exposure of aquatic ecosystems to UV is going to be subject to a number of different environmental disturbances. Stratospheric ozone depletion, acid precipitation, climate change, and clear-cut logging may all increase the exposure of freshwater ecosystems to UV radiation (Schindler 1998).

Results from our first experiment demonstrated that thick algal mats in streams can provide significant protection from UV for other organisms inhabiting the mats. Chironomids in streams with high levels of algal biomass were not sensitive to UV radiation, while chironomids in streams with low algal biomass were. These results indicate that algae provide more than just food for grazing invertebrates and that the interaction between UV, algae and grazers may involve more than a "solar cascade" (Bothwell *et al.* 1994, Williamson 1995). Algae also provide physical structure to the ecosystem, serving as substrata for colonization (Lamberti 1996) and as refugia from predation (Holomuzki and Short 1988, Power 1990) or as our results suggest, from UV exposure.

Results from our second experiment showed that clear-cut logging significantly increased the exposure of stream ecosystems to UV radiation. This increase in UV had different effects on biota in different parts of the clear-cut, stressing again that the

response of whole ecosystems to UV radiation will depend on other physical and biological variables. At the top of the clear-cut, solar radiation increased dramatically, yet the effect of logging on other physical variables, such as temperature, nutrients, and dissolved organic carbon (DOC), remained small. As a result, the benthic community responded to the increase in UV radiation. However, at the bottom of the clear-cut, the accumulated effects of logging on stream temperature, nutrients, and DOC overrode the effect of UV on the benthic community, resulting in no clear response to UV exposure.

It is likely that conditions in the logged reach of Baptiste Creek will change as the watershed slowly recovers from disturbance. As a consequence, the relative importance of factors such as increased solar radiation and increased temperature in structuring the benthic community will also change. For example, Meyer and Tate (1983) found that after an initial pulse of DOC immediately following logging, DOC export from a logged watershed was significantly lower 2 years after logging. A similar trend in Baptiste Creek would decrease the attenuation of UV radiation in the water column, thus further increasing the exposure of benthic communities to UV. Long term monitoring of streams following logging is clearly needed to fully assess the interaction between UV radiation and clear-cut logging.

Stratospheric ozone depletion, climate change and acid precipitation have been dubbed the "Big Three" stressors for boreal freshwater ecosystems (Gorham 1996, Schindler 1998). In addition to their singular effects, the "Big Three" interact with DOC to increase the exposure of aquatic ecosystems to UV radiation (Schindler *et al.* 1996a,b, Yan *et al.* 1996). Our study demonstrates that clear-cut logging represents a fourth "Big" stress for boreal aquatic ecosystems. In addition to its singular effects on streams and lakes (ie: Carlson *et al.* 1990, Hartman and Scrivener 1990, Hetrick *et al.* 1998) clear-cut logging may also interact with other anthropogenic disturbances to yield even greater impacts (Fig. 4.1).

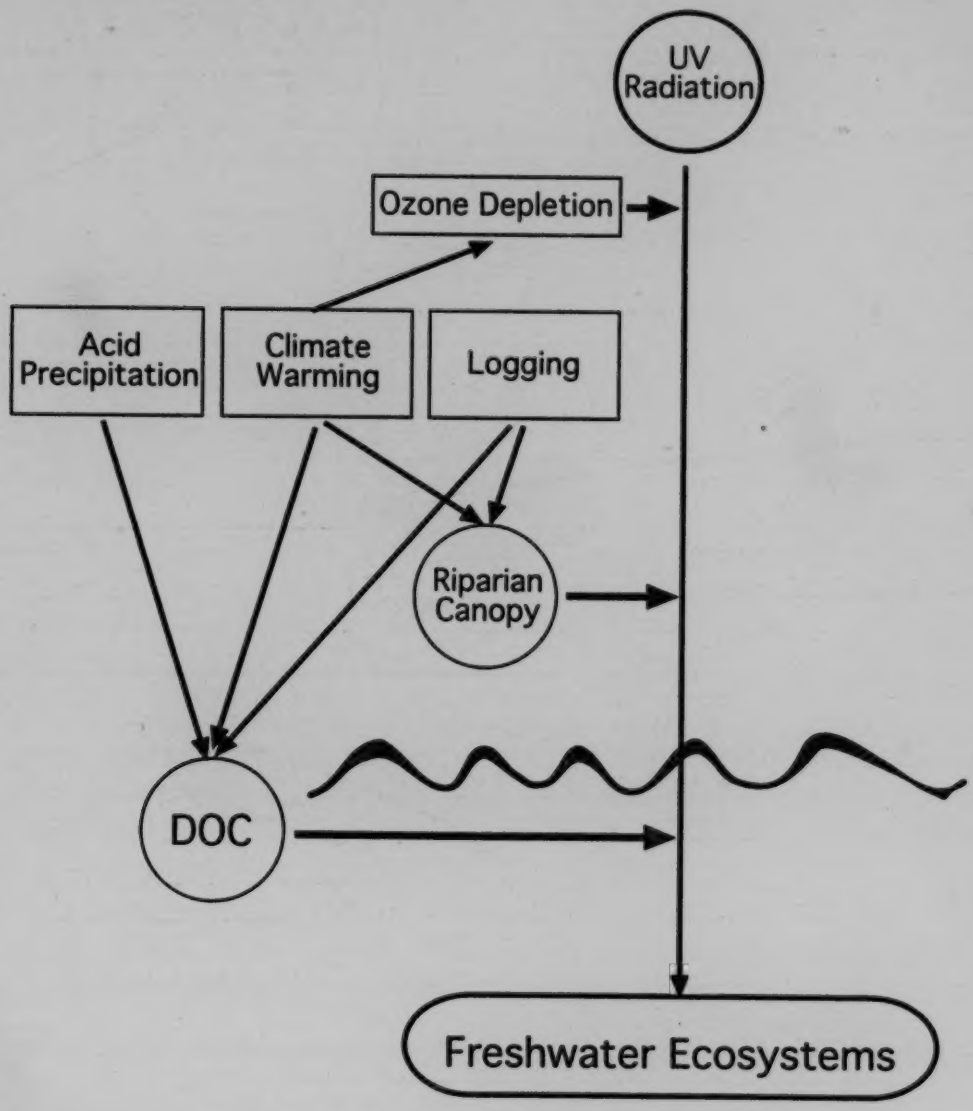

Figure 4.1: The effects of stratospheric ozone depletion, acid precipitation, climate warming, and clear-cut logging on exposure of freshwater ecosystems to UV radiation.

The BC Forest Practices Code: Effective Riparian Management?

All forestry activity in BC is regulated by the Forest Practices Code (FPC) of British Columbia (1995). Recognizing the importance of riparian areas for their high value non-timber resources and their importance in reducing or eliminating the impacts of logging on aquatic resources, the FPC has established guidelines to insure their protection and proper management. Our study in Baptiste Creek provided a direct opportunity to examine the effectiveness of the FPC in meeting its own goals for riparian management.

The FPC dictates that along all stream channels, forest companies must create a riparian management area (RMA) that must contain a riparian management zone and may contain a riparian reserve zone (Fig 4.2). Within the riparian management zone, certain constraints on forest practices are applied, and within the riparian reserve zone, all timber harvest is prohibited. The width of the RMA, and whether it includes a reserve zone, is determined by the attributes of the stream itself. Streams are classified into one of six classes (S1 to S6) based on the presence of fish, whether the stream is used as a municipal water supply, and on average channel width (Fig. 4.3). Based on this classification, S1 to S4 streams are frequented by anadromous salmonids, game fish, or threatened fish, or are used as a municipal water supply. S5 and S6 streams do not contain fish and do not provide municipal water. Based on this formula, the appropriate riparian management area for each stream channel is determined (Table 4.1). Under this scheme, Baptiste Creek was classified as an S6 stream and a 20 m riparian management area was left along each side of the stream channel.

This classification scheme was designed to meet a number of riparian management objectives. According to the FPC (BC Ministry of Forests 1995), the objective for aquatic ecosystems is to:

> *"...minimize or prevent impacts of forest or range use on stream channel dynamics, aquatic ecosystems, and water quality of all streams, lakes, and wetlands..."*

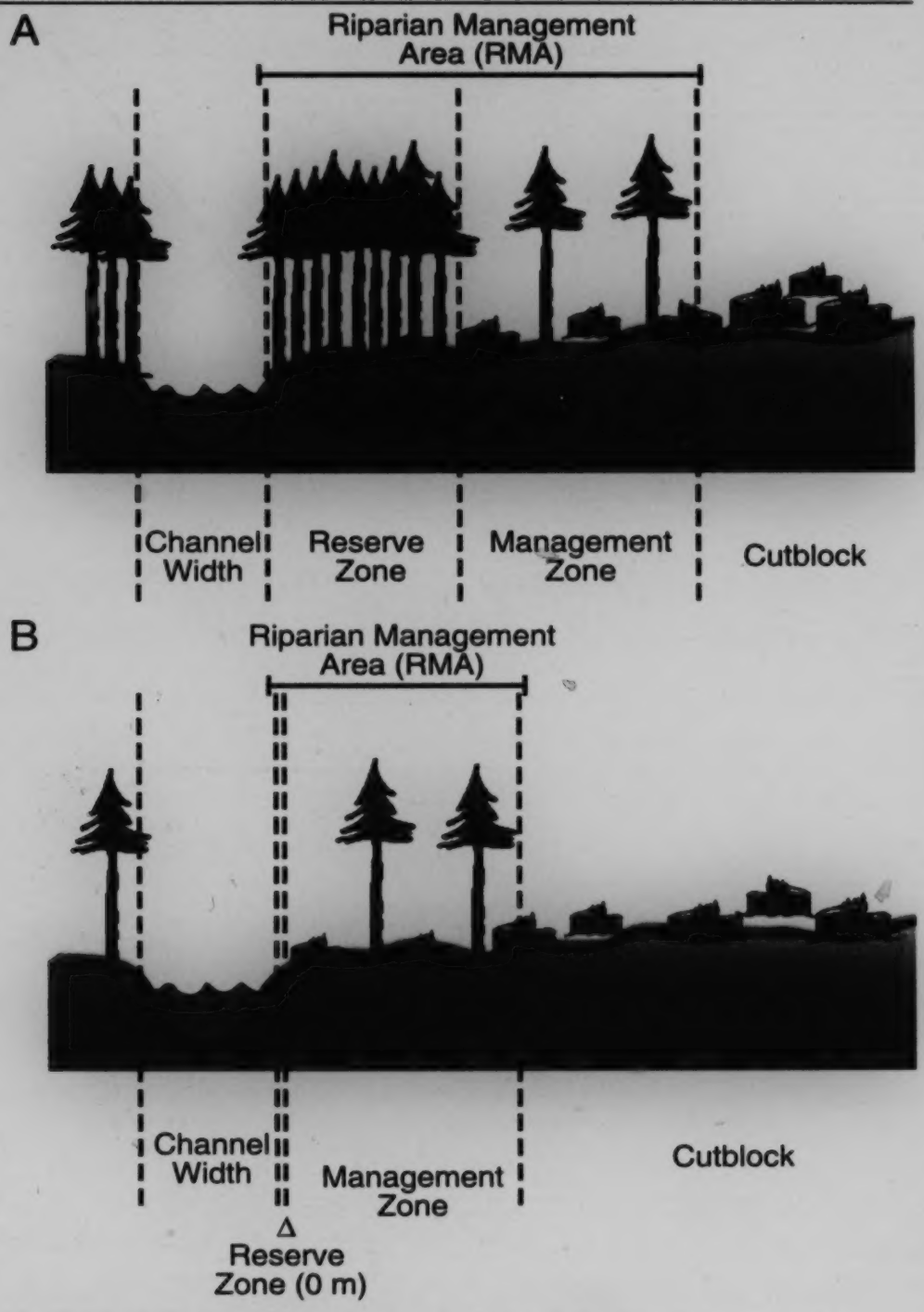

Figure 4.2: Riparian management area showing the application of a reserve and management zone (A) or a riparian management zone only (B).

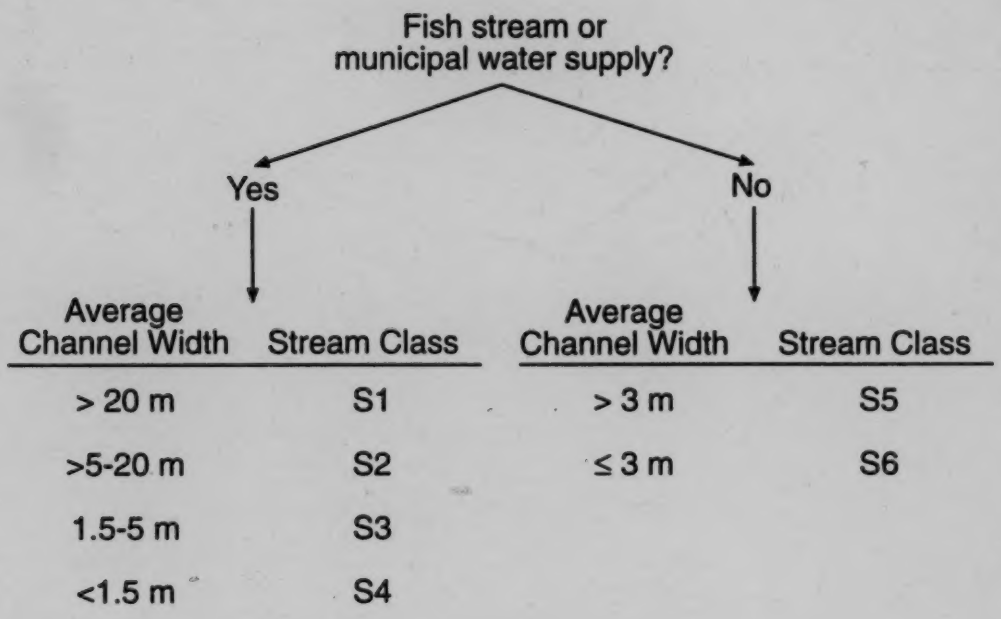

Figure 4.3: Forest Practices Code of British Columbia key to stream classification.

Table 4.1:Specified minimum riparian management area widths and composition for the six different stream classes.

Stream Class	Reserve zone width (m)	Management zone width (m)	Total RMA width (m)
S1 (large rivers)	0	100	100
S1	50	20	70
S2	30	20	50
S3	20	20	40
S4	0	30	30
S5	0	30	30
S6	0	20	20

More specifically, for small streams like Baptiste Creek, forest practices within the RMA should:

> *"...retain sufficient vegetation along streams to provide shade,reduce bank microclimate changes, maintain natural channel and bank stability and, where specified, maintain important attributes for wildlife..."*

Logging of the Baptiste Watershed followed the recommended "Best Management Practice" described by the FPC for S6 streams (BC Ministry of Forests 1995). Non-merchantable conifer trees, understory shrubs and herbaceous vegetation within 5 m of the stream channel where retained to the fullest extent possible. In the remainder of the RMA, the most windfirm 5% of codominant conifers were retained. Trees were felled and yarded away from the stream whenever possible, and slash and debris inadvertently deposited in the stream were removed. Finally, windthrow-prone trees with roots embedded in the streambank were removed, and "wildlife" trees were retained (Plate 4.1).

The RMA left along Baptiste Creek following the "Best Management Practice" failed in meeting any of the outlined goals for effective riparian management. Sufficient streamside vegetation to provide shade and reduce microclimate changes was not left

Plate 4.1: The unlogged reference (left) and clear-cut (right) reaches of Baptiste Creek the summer immediately following logging.

along the stream channel. Photosynthetically active radiation increased 670% following logging and ultraviolet radiation increased 540%. This increase in solar radiation resulted in a 2°C increase in average water temperature, and a 3.6°C increase in the daily fluctuation of temperature. In addition, water quality declined as concentrations of phosphorus, nitrogen, and dissolved organic carbon all increased with logging. Consequently, the RMA did not prevent significant impacts of logging on the stream ecosystem. Benthic invertebrate diversity declined, the abundance of chironomids increased dramatically, and the abundance of algae declined under heavy grazing pressure.

We cannot conclude with absolute certainty that the RMA left alongside Baptiste Creek did not mitigate the effects of logging. To do so, we would have had to compare the logged reach of Baptiste Creek with the RMA, to a reach logged with no buffer strip. We also cannot conclude definitively that our observations constituted significant "impacts of forest... use on stream channel dynamics, aquatic ecosystems, and water quality" (BC Ministry of Forests 1995). Obviously, we did observe significant increases in solar exposure and water temperature; and significant changes in water chemistry and the biotic community. However, the vague and unspecific wording of the FPC makes it impossible to state with any certainty whether the observed changes were severe enough to constitute a "significant impact." In defiance of this broad and unsubstantial language, we believe that our results do expose the failure of current management regulations to protect small headwater streams from the deleterious effects of clear-cut logging.

The minimum buffer width of 20 m legislated by the FPC falls within the range of 15 - 30 m generally accepted as providing adequate protection for small streams and wetlands (Castelle *et al.* 1994). However, it is assumed that these buffers consist of undisturbed, native vegetation. The approach of the FPC to retain riparian management zones where logging is permitted, but subject to minor restrictions, is flawed in several respects. Results from Baptiste Creek show that these zones do not protect streams from

logging. Instead, they impose ineffectual regulations on foresters, providing the appearance that something is being done by the industry to protect aquatic resources, when in reality the streams are unprotected. As long as the illusion remains that present RMAs are an effective way to protect small streams from logging, these systems will remain heavily impacted by logging activity.

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